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FOSSIL FISHES OF THE FAMILIES PERLEIDIDAE AND PARASEMIONOTIDAE FROM THE LOWER TRIASSIC SULPHUR MOUNTAIN FORMATION OF WESTERN CANADA

by

© Andrew G. Neuman

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

FALL, 1986

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The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research for acceptance, a thesis entitled **Fossil Fishes of the Families Perleididae and Parasemionotidae from the Lower Triassic Sulphur Mountain Formation of Western Canada** submitted by **Andrew G. Neuman** in partial fulfilment of the requirements for the degree of **Master of Science.**

.....
(Supervisor)

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DATED Oct. 7, 1986

Abstract

Fossil fishes of the families Perleididae and Parasemionotidae are reported from the Lower Triassic Sulphur Mountain Formation of western Canada. A new species of the subholostean family Perleididae is described and this family is used to help establish polarities for characters seen in the family Parasemionotidae. The characters of most interest are those related to the nature of the opercular apparatus, jaws, ethmoid region of the skull, and pectoral girdle.

The evolutionary significance of the family Parasemionotidae has been recognized for some time, as the family appears to represent an intermediate stage of evolution between primitive chondrosteans and higher actinopterygians. Several kinds of parasemionotids are present in the Sulphur Mountain Formation. One of these, Albertonia cupidinia, has previously been briefly described. This species is discussed in more detail here and a new species is added to the genus Albertonia. A second group of parasemionotids from western Canada is referred to the genus Watsonulus and a new genus is added to the family Parasemionotidae.

Current theories regarding the relationships of the family Parasemionotidae are discussed as this is the subject of an ongoing debate. A revised diagnosis for this family is provided and a review of all genera that have been included in the family Parasemionotidae in recent

years is made in an attempt to establish which of these genera should rightfully be placed in the family and which should not.

Acknowledgements

I thank the many people who have contributed to the completion of this project. My supervisor, Dr. M.V.H Wilson, supplied much help and guidance throughout the study. An earlier draft of this thesis was critically reviewed by Dr. Wilson and the other members of my supervisory committee, Drs. B.D.E. Chatterton, R.C. Fox, B.G. Naylor and J.S. Nelson.

Loan of specimens was generously arranged by Drs. B. Schaeffer and J. Maisey of the American Museum of Natural History, Dr. D. Russell and Mr. R. Day of the National Museums of Canada, Drs. B.G. Naylor and D. Brinkman of the Tyrrell Museum of Palaeontology and Dr. M. Wilson of the University of Calgary. Geological and locality information was supplied by Drs. D. Gibson and B. Richards of the Institute of Sedimentary and Petroleum Geology, Geological Survey of Canada.

I also thank Allan Lindoe for his help and friendship in the field and for his valuable technical advice in the laboratory. He also supplied the photographs that appear in Figures 5 and 7. My thanks also go to Rosemary Neuman for drafting Figure 2 and for offering knowledgeable advice on the other maps, and to Robert Williams for advice and discussion on several aspects of the thesis.

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Most of all I thank my wife Becky and my son Michael for their support and understanding throughout the course of this project.

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Abbreviations

A) Abbreviations used in the text are as follows:

AMNH- American Museum of Natural History. New York, New York.

BM(NH)- British Museum (Natural History). London, England.

EM- L'École des Mines de Paris. Paris, France.

NMC- National Museum of Natural Sciences, National Museums of Canada. Ottawa, Ontario.

TMP- Tyrrell Museum of Palaeontology. Drumheller, Alberta.

UAVP- University of Alberta, Laboratory for Vertebrate Paleontology, Departments of Geology and Zoology. Edmonton, Alberta.

UC- Geology Department, University of Calgary. Calgary, Alberta.

YPM- Peabody Museum of Natural History, Yale University. New Haven, Connecticut.

B) Abbreviations used in the figures are as follows:

1) Geology:

I- Ishbel Group

L- Llamna Member

M- Rundle Group

P- Paleozoic rocks

Tr- Triassic Sulphur Mountain Formation

V-P- Vega-Phroso Siltstone Member

W- Whistler Member

2) Anatomy:

Ang- angular

Ao- antorbital

Br- branchiostegals

Cl- cleithrum

Co- coronoid

D- dentary

Dh- dermohyal

Dpt- dermopterotic

Dsph- dermosphenotic

Dspl- dentosplenial

Exsc- extrascapulars

fhy- foramen for hyomandibular nerve

Fr- frontal

Gu- gular

hp- horizontal pit line

Io- infraorbital

ioc- infraorbital canal

Iop- interopercle

mc- mandibular canal

Mx- maxilla

Na- nasal

na_1- first naris

na_2- second naris

Op- opercle

opp- opercular process

P- parietal

Part- prearticular

Pmx- premaxilla

Pop- preopercle

popc- preopercular canal

Pr- postrostral

Pt- posttemporal

Qj- quadratojugal

Ros- rostral

Sang- surangular

Scl- supracleithrum

Smx- supramaxilla

So- supraorbital

soc- supraorbital canal

Sop- subopercle

Spi- spiracular

St- supratemporal

stc- supratemporal canal

t- teeth

v- vomer

vp- vertical pit line

1. Introduction

A) Historical Background

Triassic fishes have been known from western Canada since first reported by L.M. Lambe in 1914 from the Banff area of Alberta. His original paper described Platysomus (Bobasatrania) canadensis based on a large fossil fish that was housed in the Banff Museum (Lambe, 1914). The collection locality of this specimen is uncertain, but the specimen is believed to have come from the vicinity of Johnston's Creek.

Lambe later reported specimens of several other genera from the Massive and Johnston's Creek areas, both near Banff, Alberta (Lambe, 1916). Since that time additional collections have been made from the Massive site by P.S. Warren and W.F. Ferrier in 1921 and by J.P. Day in 1924 (Raymond, 1925). During preparations for twinning of the Trans-Canada Highway in the early 1980's, a new site near Massive was discovered and a small collection was made by Dr. D. Fedje (Archeological Office of Parks Canada) and Dr. B. Richards (Geological Survey of Canada). This site has been named the Eisenhower Junction site. It has also been visited by Dr. M.V.H. Wilson from the University of Alberta, Dr. D. Brinkman from the Tyrrell Museum Of Palaeontology, Dr. M.C. Wilson from The University of Calgary and the author.

A number of additional Lower Triassic sites are

known from western Canada that produce fossil fish material. Articulated specimens have been found at some of these sites (see Fig. 1 for summary of these localities).

The best known of these Lower Triassic fish localities occur in the Ganoid Range near Wapiti Lake, B.C. (Fig. 2). The Wapiti Lake sites were first discovered by L.R. Laudon and a group of students from the University of Wisconsin in 1947 (Laudon, et al., 1949). They reported finding "excellently preserved specimens of ganoid fishes" from the steep slope above Fossil Fish Lake in the Ganoid Range, but because of transportation difficulties, none were collected.

In 1948, C.M. Sternberg visited the site for the National Museums of Canada and collected a number of specimens. Several dozen additional specimens were collected by Imperial Oil Enterprises, Ltd., in 1957, in conjunction with A. McGugan, then at Queen's University in Kingston, Ontario (Forbes and McGugan, 1959). These specimens are now housed at the National Museums of Canada in Ottawa.

During the 1960's, several collections were made from the Wapiti Lake area, including those of B.R. Pelletier of the Geological Survey of Canada (Pelletier, 1963), A. McGugan from the University of Calgary, J.R. Nursall from the University of Alberta, and a large joint expedition from the National Museums of Canada and the American Museum of Natural History led by G. Stucker and H.

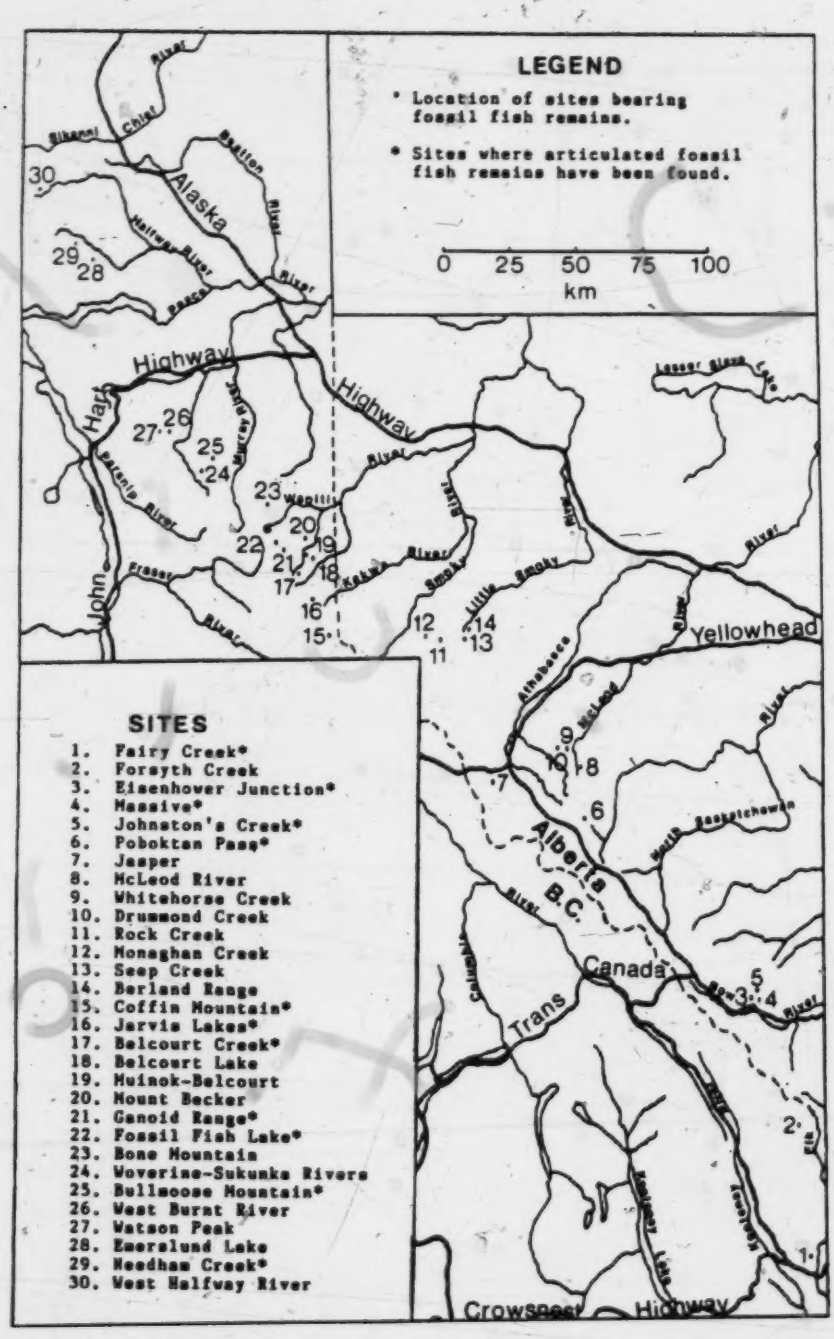

Fig. 1: Early Triassic localities in western Canada that bear remains of fossil fishes.

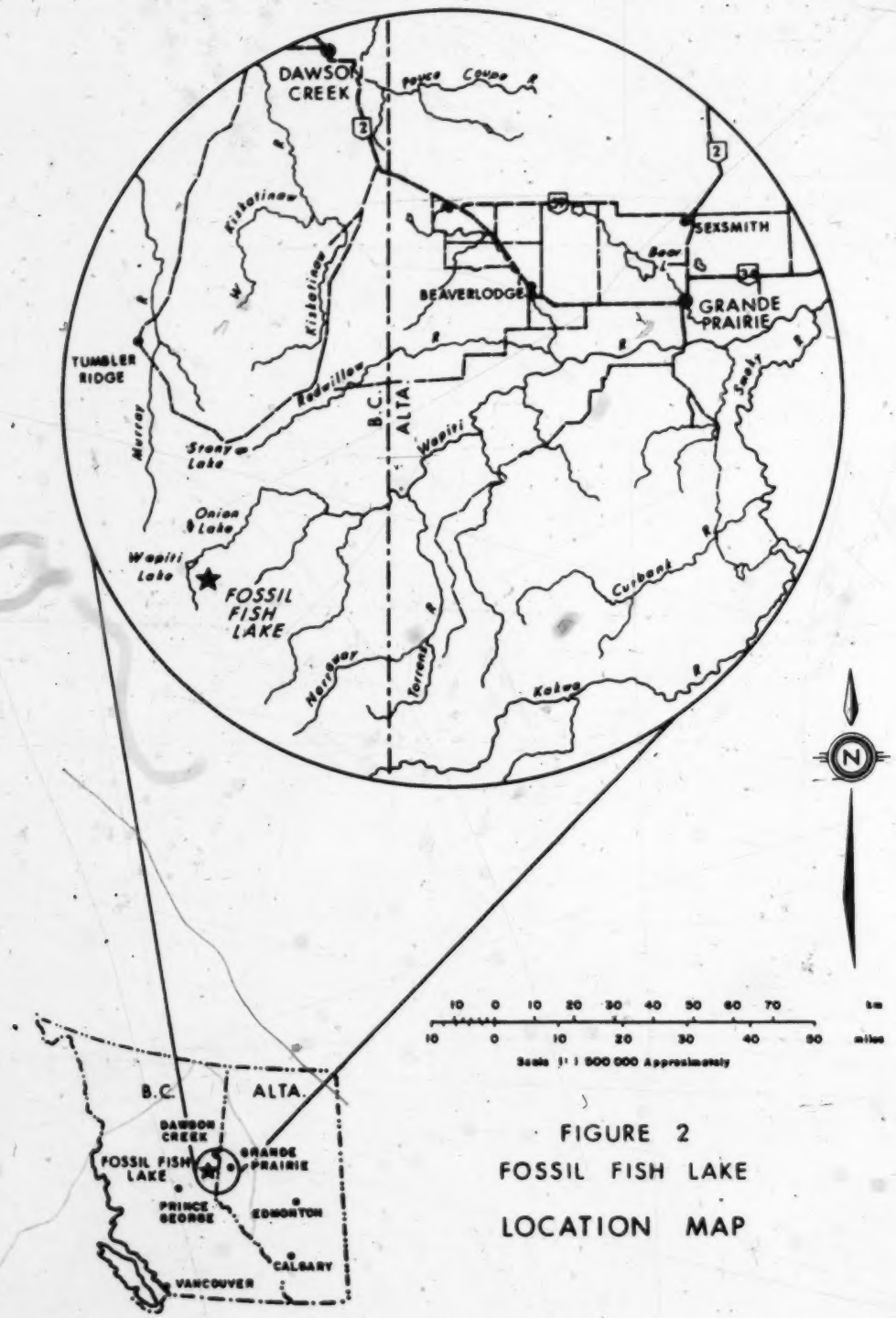

FIGURE 2
FOSSIL FISH LAKE
LOCATION MAP

Champagne (Schaeffer and Mangus, 1976). These collections were reported by Gardiner (1966), and were used in the writing of a preliminary report on Lower Triassic fishes from western Canada by Schaeffer and Mangus (1976).

Following the 1976 publication, interest in the Wapiti Lake Triassic fossil fish sites was renewed and in 1983 a joint expedition from The University of Alberta and the Tyrrell Museum of Palaeontology visited the area. This expedition was led by Dr. M.V.H. Wilson and Dr. D. Brinkman; it was very successful and a large number of specimens was collected. Further collections from the area were made by the author and L.A. Lindoe from The University of Alberta in 1984 and 1985.

A commercial fossil and mineral company from Calgary, Korite Minerals, Ltd., also made collections from the Ganoid Range during the early 1980's.

The present study is based mainly on the collections made during the 1980's, but specimens from The University of Alberta, The University of Calgary, the National Museums of Canada and the American Museum of Natural History, collected prior to this time, are included.

B) Systematic Background

The first purpose of this study is to supply detailed descriptions of previously undescribed Early Triassic fishes from western Canada. Previous descriptions of Canadian fishes from this time period are brief (Lambe, 1914; 1916; Raymond, 1925; Warren, 1936; Russell, 1951; Schaeffer and Mangus, 1976), and are based mainly on incomplete material.

Three new species, two parasemionotids and one perleidid, are described here on the basis of fairly well-preserved material. New specimens are assigned to the species Albertonia cupidinia (Lambe, 1916), and this species is described in more detail than in previous descriptions. Some parasemionotids from western Canada are compared with the Madagascar species Watsonulus eugnathoides. This species shows significant variation in the structure of the preopercle, in the shape of the body and in some features of the skull. This variation indicates that there is probably more than one taxon represented.

The second aspect of the study is to comment on a continuing controversy about the phylogenetic relationships and generic composition of the family Parasemionotidae. This family has variously been placed as the sister group of the amiid line (Patterson, 1973), of the amiid and teleost lines (Gardiner, 1967) or of all other higher actinopterygians (Olsen, 1984). The several

options for the possible relationships of the family Parasemionotidae are tested, and the analyses of Gardiner, Patterson and Olsen are discussed. Data from the new species described here, and from other members of the family Perleididae described in the literature, are used to help establish the polarities for some of the characters used in the discussion of the relationships of the parasemionotids.

Data from the literature and from the new species of parasemionotids are used to delineate the family Parasemionotidae and to establish its generic composition. Besides the traditional members of the family, Parasemionotus, Watsonulus, Ospia, Broughia and six additional, poorly known genera from Madagascar, a number of other genera have been assigned to this family in recent years. These genera are generally placed in other taxa. A revised diagnosis for the family Parasemionotidae is provided to help clarify which of these genera should be placed in the family Parasemionotidae, and which should not.

2. Methods

A) Preparation of specimens

The specimens used in this study are preserved in calcareous siltstones and shales that generally split along horizontal planes of weakness created by the fossils themselves. Mechanical preparation was readily accomplished with pneumatic tools and dental picks. The specimens appear to be superficially well preserved, but closer inspection reveals that the bone is often broken or missing. Details of the skull not observable in the original material were highlighted by removing the bone fragments with dilute hydrochloric acid and taking latex, silicone or polysulphide peels of the remaining impressions.

Schaeffer and Mangus (1976) and Olsen (1984) used a polysulphide rubber compound called Smooth-On to produce peels of specimens that had been etched with hydrochloric acid. The rubber used in this study is Smooth-On polysulphide rubber flexible mold compound (FMC-201). This material is easily removed from the specimens and does minimal damage. The following procedures were followed to maximize the quality of the peels.

First, the surface of the rock around the specimen was treated with a liberal coat of liquid cement to protect it from the acid used to etch the specimen. The coating prevents the rock from becoming too porous and

allowing excessive penetration by the rubber, which makes the peel more difficult to remove. When all of the bone was removed, the specimen was thoroughly rinsed in water, and was soaked in baking soda and water for approximately 48 hours to neutralize the acid. This is necessary because the Smooth-On compound will react with residual acid and will not set.

Following acid preparation, the surface of the prepared specimen was covered with a very thin coat of liquid cement to protect it from damage during subsequent procedures. A release agent of liquid detergent or soap and water was then applied to the surface of the specimen and the surrounding rock. This release agent was allowed to soak in and dry. Increased details were exposed when a thin coat of the polysulphide rubber was poured over the specimen and it was placed into a vacuum chamber to remove air bubbles. Approximately 0.5 to 1.0 cm of rubber was the optimal thickness.

B) Measurements

Measurements and counts taken are generally after those of McCune (in press). When conventional measurements could not be reliably taken, landmarks were chosen that could be repeatedly located, and measurements that could be easily reproduced were used.

The measurements were taken by locating landmarks using a Wild M3 dissecting scope at a magnification of

32X, and marking these landmarks with a small spot of waterproof paint. Distances between the landmarks were then measured using calipers or a steel ruler. The following measurements and counts were taken for each specimen:

BD- Body depth, measured in a straight line from insertion of first fringing fulcral scale of dorsal fin to insertion of first fringing fulcral scale of anal fin.

BD/SL- Ratio of body depth divided by standard length.

HD- Skull depth, measured from sensory canal at intersection of supratemporal and posttemporal bones to most ventral point of intersection between dentary and angular.

HD/HL- Ratio of skull depth divided by skull length.

HL- Skull length, measured from anterior tip of premaxilla to most posterior point of intersection of opercle and subopercle.

HL/SL- Ratio of skull length divided by standard length.

MD/ML- Ratio of maximum depth of maxilla divided by maximum length of dentigerous margin of maxilla.

ML/HL- Ratio of maximum length of dentigerous margin of maxilla divided by skull length.

ML/POPD- Ratio of maximum length of dentigerous margin of maxilla divided by depth of preopercle, measured from dorsal end of preopercular canal to anteroventral end of preopercular canal.

OPL/HL- Ratio of length of opercle, divided by skull length; length of opercle measured from most anterior

point of articulation between opercle and subopercle, to most posterior point of articulation between these two bones.

OPL/OPD- Ratio of length of opercle divided by maximum depth of opercle.

SL- Standard length, measured from anterior tip of premaxilla to insertion of first lepidotrichium in caudal fin that curves dorsally from its attachmemt with caudal peduncle; this lepidotrichium occurs at approximately the level of the lateral line.

SAF- Number of scale rows counted from posterior border of extrascapular series to insertion of first fringing fulcral scale of anal fin.

SDF- Number of scale rows counted from posterior border of extrascapular series to insertion of first fringing fulcral scale of dorsal fin.

TS- Total number of scale rows counted along lateral line canal, from posterior border of extrascapular series to base of caudal fin; base of caudal fin taken as point of insertion of first fringing fulcral scale of this fin.

AR- Number of lepidotrichia in anal fin; first lepidotrichium counted is first one that runs complete length of fin; this lepidotrichium is segmented but does not branch distally.

CR- Number of lepidotrichia above midline on caudal fin; first lepidotrichium counted is first one that shows

definite upward curvature at its insertion.

DR- Number of lepidotrichia in dorsal fin; first lepidotrichium counted is first one that runs complete length of fin; this lepidotrichium is segmented but does not branch distally.

P_1R- Number of lepidotrichia in pectoral fin.

P_2R- Number of lepidotrichia in pelvic fin.

P/SL- Ratio of length of pectoral fin divided by standard length; length of pectoral fin is measured from insertion of longest ray onto pectoral girdle to most distal point of ray.

C) Discrimination of species

A large sample of specimens referred to the family Parasemionotidae, ranging in size from 50 to 400 mm, has been collected from the Triassic of western Canada. These specimens are very consistent in some of their characters, but show important variation in others. The following information was used to help discriminate among the various species of parasemionotids.

1) Meristics

The meristic data obtained from the specimens did not prove to be particularly useful for identification of species. There is little difference among the taxa present in numbers of scale rows or in numbers of fin rays.

2) Analysis of body shape

Body shape initially appeared to show variation among the groups studied. A variety of methods is available for comparison of body shapes in fishes but the ones that appeared to be most applicable to this study were those used by McCune (in press) and Wilson (1983). A combination of their methods seemed to give the best results here.

Procedure.- Body outlines were drawn and analysed using a computer program written by M.V.H. Wilson. This program uses a digitizer to enter the shapes of the fishes to the computer, and a plotter to print the shapes to hard copy. The operation of this program and the equipment necessary are described by Wilson (1983). Certain modifications have been made to the original program (Wilson, personal communication, 1986) to include the locations of strategic points on the body outlines, such as origins of fins. These points were incorporated by McCune (in press) in her analyses of body shape.

The body shapes can be plotted at relative sizes or scaled to the same size, so that the shapes of specimens of different sizes can be compared. The shapes can be plotted individually, or can be superimposed (Fig. 3).

Problems.- Many of the specimens examined in this study are distorted by oblique compression. This can give the impression of increased or decreased body depth. If the origins of the dorsal and anal fins are located on the dorsal and ventral margins of the body, the distortion of

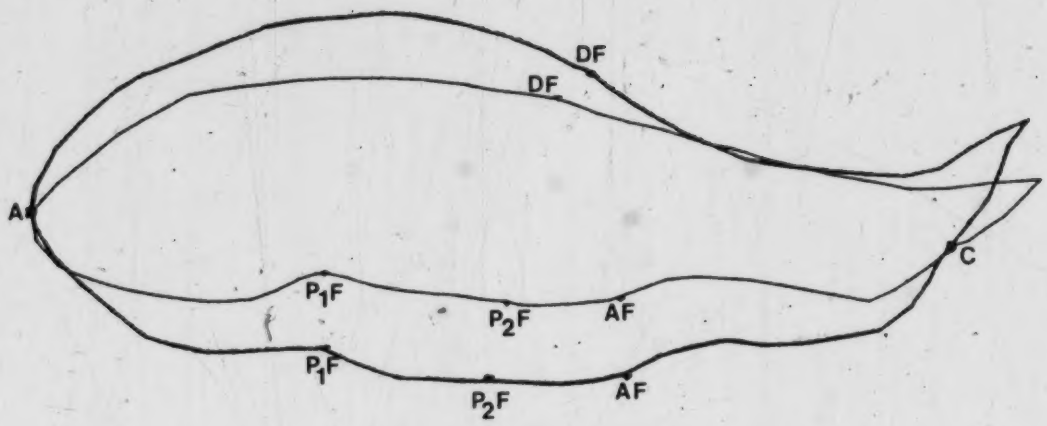

Fig. 3: Digitized outlines of Watsonulus cf. W. eugnathoides (thin line) and Laudonia brevicephala gen. et sp. nov. (thick line) to show differences in body shape. A- anterior tip of premaxilla, AF- origin of anal fin, C- point of insertion of first lepidotrichium that curves dorsally from its insertion, DF- origin of dorsal fin, P_1F- origin of pectoral fin, P_2F- origin of pelvic fin.

the fish is minimal and the outlines are most likely to be accurate. If the dorsal and anal fins appear on the dorsolateral or ventolateral surface of the body outline, oblique compression has occurred and the outline is distorted. By plotting the positions of median and paired fins on to the body outline, a more reliable estimate of the amount of distortion can be realized and a more accurate estimate of the body shape can be obtained.

Results.- There is often overlap in body shape between species, so by itself, body shape is not a consistent discriminator. It can be a useful character for distinguishing between species of the family Parasemicnotidae from western Canada, however, when used in conjunction with other characters. More work on larger sample sizes is needed before the full effectiveness of this technique can be realized.

3) Shapes of skull bones

The most useful criteria for discriminating among the species of parasemionotids from western Canada include the sizes, shapes and relationships of the various skull elements. Many parasemionotid genera and species are based on descriptions of the skull bones, especially those of the opercular apparatus. Analysis of the morphometrics of the skull elements of the specimens in this study has also been useful for discriminating between species. The computer program used for analysis of body shape was also

useful for comparing preopercles from various parasemionotids (Fig. 11).

4) Length and position of fins

The basic meristic patterns and locations of fins are consistent among the species in this study, but there is notable difference in the length of the pectoral fins. A comparison was made between the lengths of the pectoral fins and the standard lengths of the fishes, and it was found that the genus Albertonia is discriminated from the other genera in the family Parasemionotidae partially by the length of the pectoral fins (Fig. 4).

D) Definition of terms

The following terms are used in the chapter entitled "Discussion of Phylogeny", and are defined here:

Chondrostean- Actinopterygian fishes of a relatively primitive grade that do not possess any of the synapomorphies that unite the more derived actinopterygians. The subclass Chondrostei of Patterson (1973).

Subholostean- Fishes intermediate in grade between chondrosteans and higher actinopterygians. These fishes show a combination of primitive and derived characters but do not show the synapomorphies that unite the higher actinopterygians. This term is not presently used in any formal classification, but is discussed by Schaeffer (1973).

Holostean- Fishes sharing a number of derived characters not present in chondrosteans, but which are not a holophyletic group. These fishes are of a general grade in actinopterygian evolution whose upper and lower boundaries can only be arbitrarily defined. The term Holostei has been dropped from most formal classifications (Patterson, 1973).

Teleostean- Higher actinopterygians that show shared derived characters that unite them and separate them from chondrosteans and holosteans. The subdivision Teleostei of Patterson (1973).

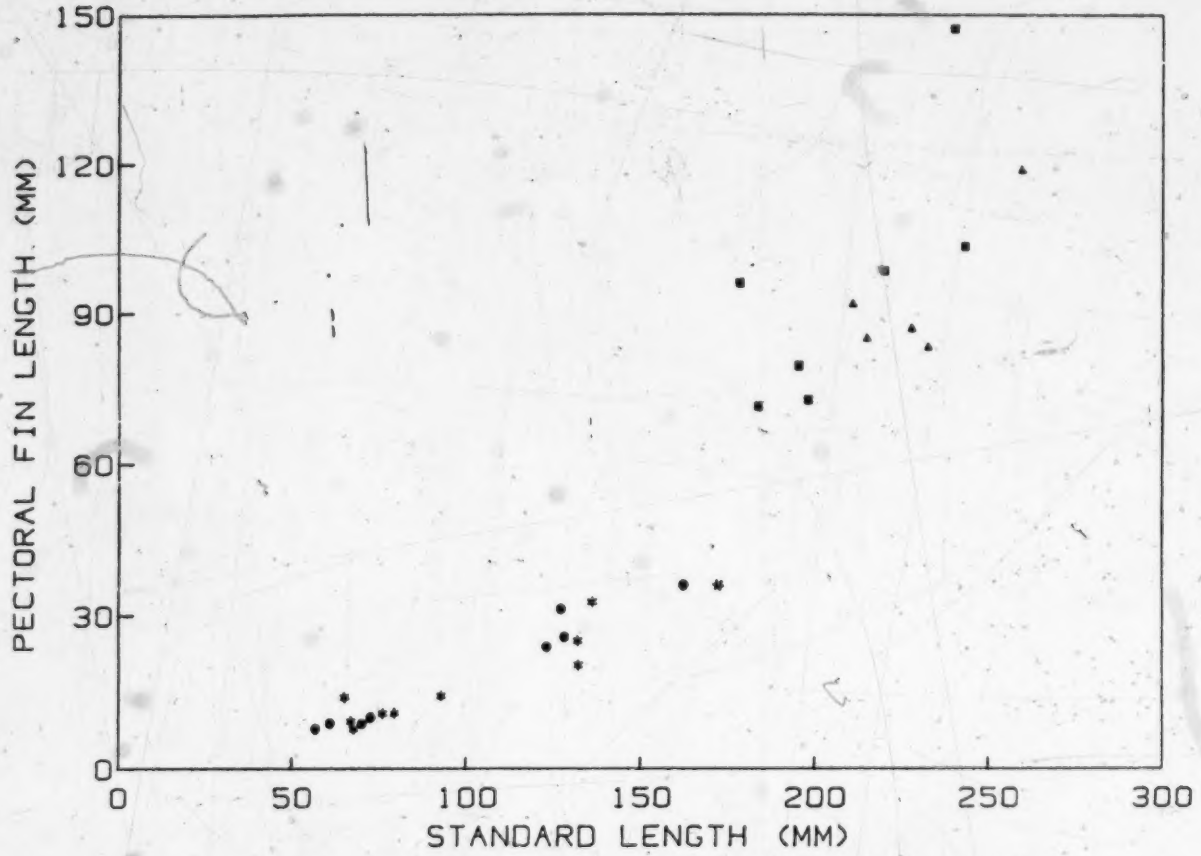

Fig. 4: Comparison of pectoral fin length to standard length in Watsonulus cf. W. eugnathoides (stars), Laudonia brevicephala gen. et sp. nov. (circles), Albertonia cupidinia (squares) and A. lambei sp. nov. (triangles).

3. Geological Occurrence

Several specimens described here as Albertonia cupidinia were collected from a railway cut approximately 21 km west of Banff, Alberta along the Canadian Pacific Railway at Massive (51°13.5'N, 115°47.8'W) (Fig. 1). The specimens come from dark grey, resistant, sandy shales that weather brownish to buff grey and are of Lower Triassic age according to Dr. G.H. Girty of the United States Geological Survey (Lambe, 1916).

Kindle (1924) named the Lower Triassic rocks of this area Spray River Formation and Warren (1945) later subdivided the formation into an upper Whitehorse Member and a lower Sulphur Mountain Member. Irish (1951) and Mountjoy (1960) elevated these members to formational status. The fossil fishes occur in the lower part of the Sulphur Mountain Formation, which Gibson (1968) further subdivided into Vega and Phroso Siltstone members in the area north of Athabasca River. He later extended this division to the Banff area (Gibson, 1969). It is not certain which of these two members contains the fossil fishes at the Massive site and further work is needed to establish correctly the exact location of the fossil fishes within the Sulphur Mountain Formation. Invertebrate fossils collected at Spray River Gorge near Banff establish the age of the Phroso Siltstone Member as Griesbachian and that of the Vega Siltstone Member as Smithian (Gibson, 1974).

The main collection of fossil fishes discussed in this paper was obtained from the Ganoid Range in the vicinity of Wapiti Lake, B.C., approximately 150 km southwest of Grande Prairie, Alberta (54°30.5'N, 120°43'W) (Fig. 2). The Ganoid Range is one of the eastern ranges of the northwest-southeast trending ridges comprising the Canadian Rocky Mountains (Schaeffer and Mangus, 1976). It is located approximately 5 km southwest of the thrust front of Paleozoic rocks in the Canadian Rockies of this area (Laudon, et al., 1949). The structure of the area consists of a series of tightly folded thrust-fault blocks that trend approximately N48°W (Laudon, et al., 1949). The structure of the Ganoid Range itself is approximately parallel to this general trend.

The study area is a ridge approximately 8 km long, composed of an overturned fold that has a northeast-southwest strike. The west side of the ridge is formed by strata that are right side up with Triassic rocks overlying late Paleozoic rocks (Fig. 5A). The eastern side of the ridge is formed by the overturned eastern arm of the fold, so that the late Paleozoic rocks overlie the Triassic rocks in some regions of the study area. The actual shape and structure of the fold can be seen on the ridge at the south end of a cirque about half way along the Ganoid Range, southeast of Schaeffer and Mangus's (1976) study area (Fig. 5A). It is also figured

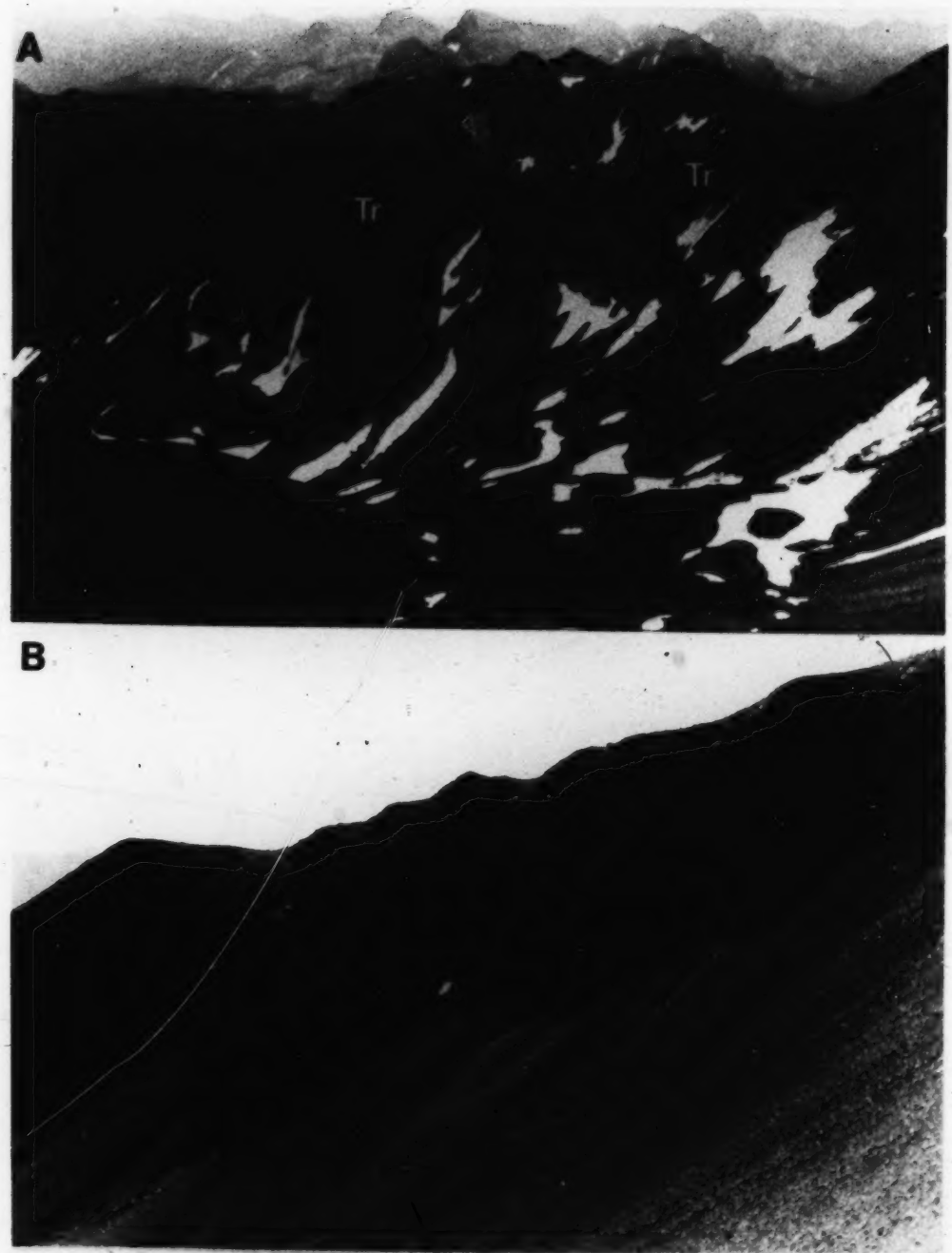

Fig. 5: Folded and deformed strata on the Ganoid Range.
A. Overturned fold axis in the centre of D cirque (see Fig. 6).
B. Overturned east arm of C cirque (see Fig. 6) showing high degree of deformation of rocks. (Abbreviations are listed on p. xiii).

by Laudon, et al. (1949, text-fig. 8).

Locally within the ridge on the eastern arm of the fold, very high intensity deformation has resulted in additional folding and faulting. An example of this is discussed by Shaeffer and Mangus (1976): "A major fault cuts diagonally across the cirque face and accounts for further discontinuity, displacement, and repetition of beds. Locality 1 is a dislocated block found just below the fault, about 400 feet below the contact." Extensive folding, distortion and repetition of beds can also be seen in R and C cirques and along the east arm of the fold in D cirque (Fig. 5B). This repetition of beds is largely resposible for the high concentration of fish fossils in the talus of these areas.

The sites discussed in this study are shown in Fig. 6 and are located in cirques labelled X, R, F, C, A and D. The highest concentrations of specimens discovered to date have come from R, F, and C cirques, all of which are in the vicinity of a small lake appropriately named Fossil Fish Lake. Cirque C is also the location of a commercial fossil quarry operated by Korite Minerals, Ltd. of Calgary, Alberta.

The Triassic section in the study area consists of only the Sulphur Mountain Formation and the lower part of the Whitehorse Formation as described by Gibson (1972; personal communication, 1985). The Sulphur Mountain Formation is divided into three members in ascending

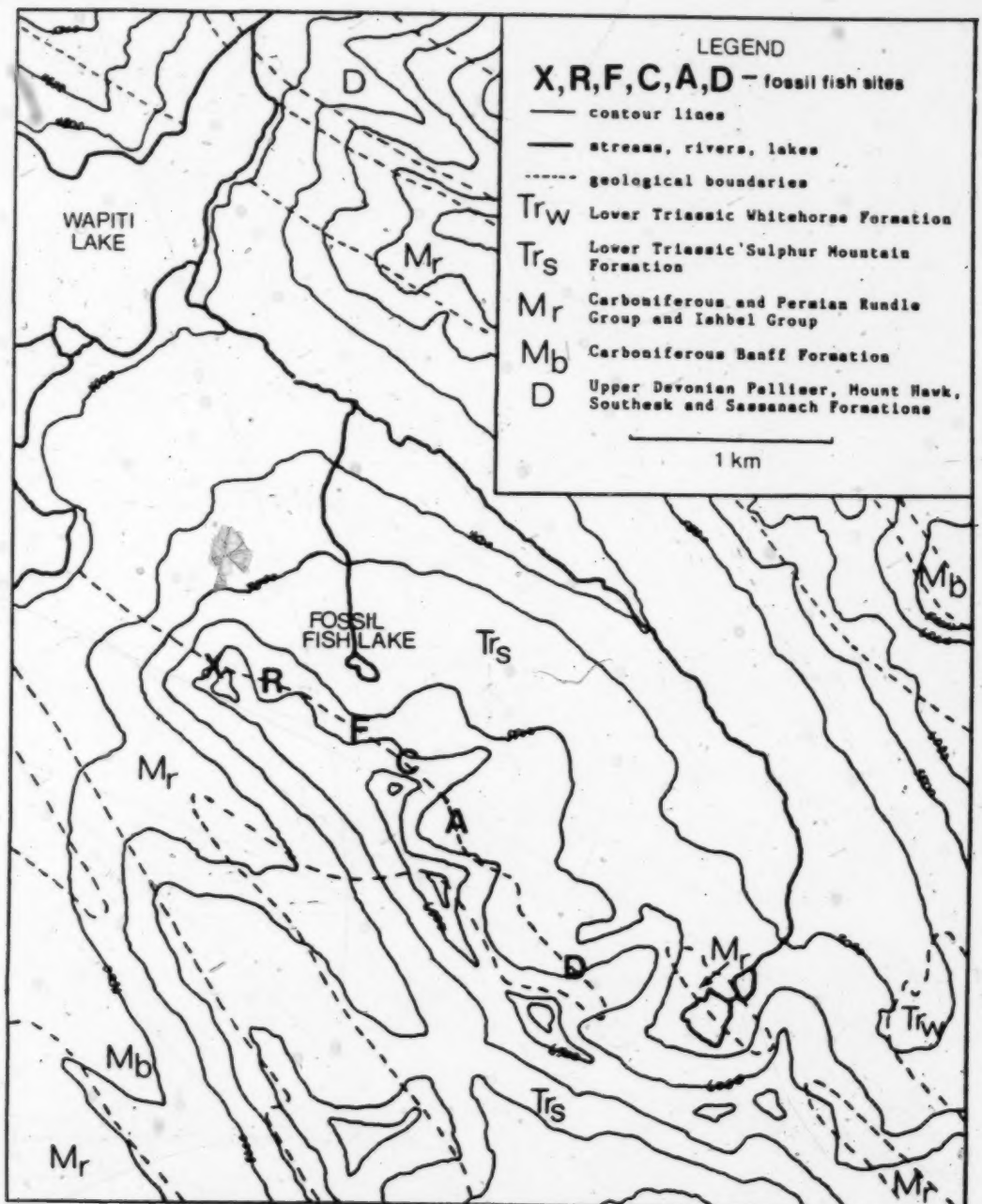

Fig. 6: Detailed map of Wapiti Lake area, British Columbia showing general stratigraphy and sites that bear fossil fish remains.

order: Vega-Phroso Siltstone Member, Whistler Member, and Llamna Member (Fig. 7A). The formation comprises a sequence of siltstones, silty limestones, minor shales, dolostones, and very fine grained sandstones that weather to a characteristic dark grey to orange-brown (Gibson, 1972). The fossil bearing strata themselves belong to the Vega-Phroso Siltstone Member (Gibson, 1972). This member is made up of a dark-brownish grey to rusty-brown, shaly to flaggy-weathering sequence of dolomitic to calcareous siltstone, finely crystalline to bioclastic limestone, silty shale, and minor amounts of very fine-grained quartz sandstone (Fig. 7B). The name Vega-Phroso is a combination of the two names used for the two distinct Early Triassic members of the Sulphur Mountain Formation in the Jasper region of Alberta (Gibson, 1968).

The lower 25 to 50 m of the Vega-Phroso Siltstone Member are remarkably uniform at most sections. Strata consist of recessive, partly talus-covered, finely laminated, thin-bedded, very carbonaceous to argillaceous, dolomitic, quartz siltstone and silty shale. Strata of similar physical and mineralogical characteristics have been recognized in other regions of the Rocky Mountains and called the Phroso Siltstone Member in the south (Gibson, 1968) and the Grayling Formation in the north (Gibson, 1971). However, in this region the typical Phroso-like facies is not confined to the lower 50 m but is also found interfingering with beds of the more

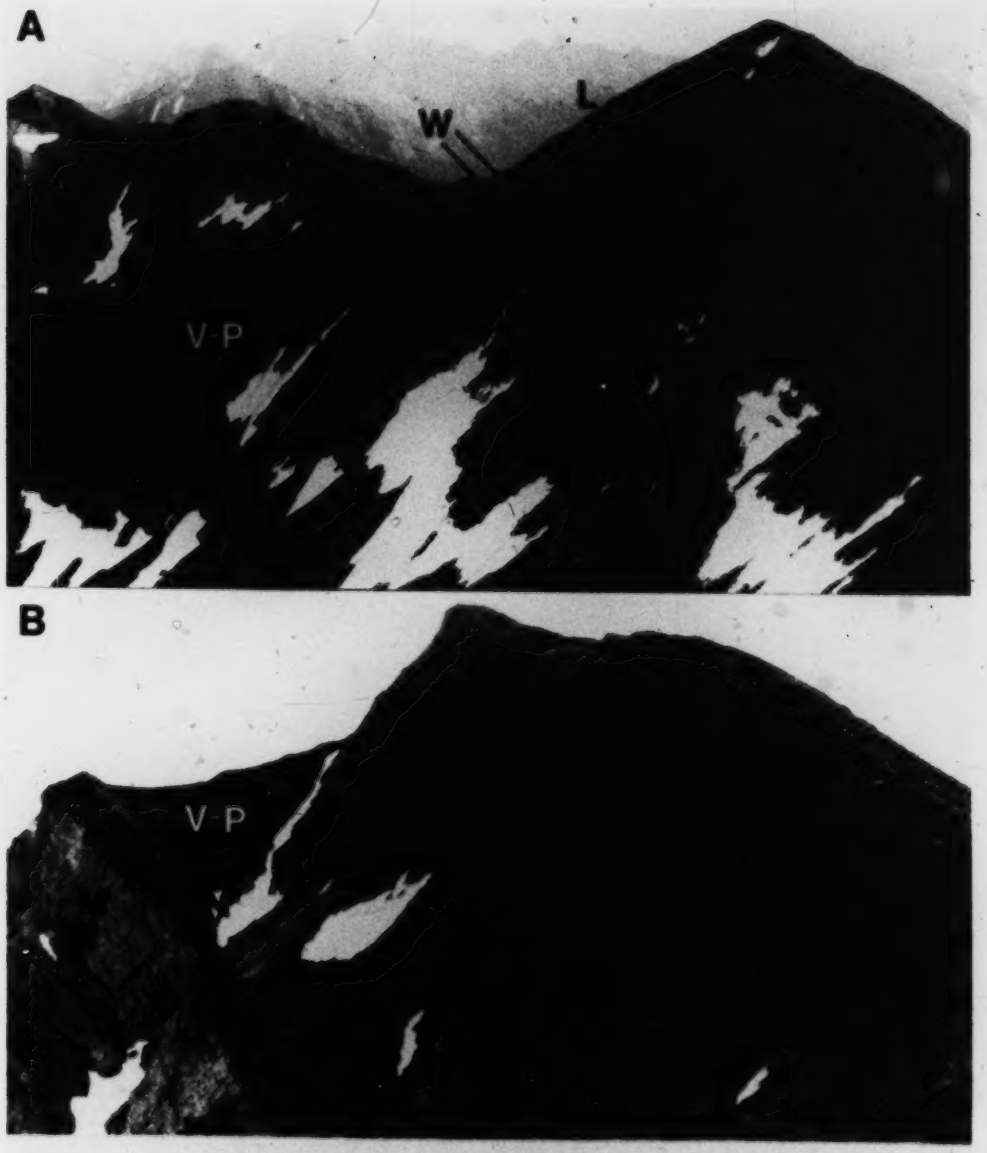

Fig. 7: Lithology and stratigraphy of the Sulphur Mountain Formation.
A. Complete section of Sulphur Mountain Formation outcropping on the west arm of the fold in D cirque (see Fig. 6).
B. Typical lithology of the Vega-Phroso Siltstone Member, overlying the Ishbel Group (Permian) and Rundle Group (Mississippian) in A cirque (see Fig. 6).
(Abbreviations are listed on p. xiii).

resistant Vega-like facies higher in the section, so the combination of Vega and Phroso Member names is used (Gibson, 1972). A detailed description of the lithology of the Vega-Phroso Siltstone Member is given by Gibson (1972, pp.6-7).

In the study area, the Vega-Phroso Siltstone Member ranges in thickness from about 225 to 250 m. It disconformably overlies porous, calcareous and glauconitic sandstones of the Upper Permian Mowitch Formation (McGugan and Rapson-McGugan, 1976). In some sections the Mowitch is difficult to distinguish from the older Ranger Canyon Formation, which is chiefly composed of a dark grey to white chert, because they are gradational. The uppermost bed, however, is usually a sandstone with conspicuous black phosphatic nodules (McGugan and Rapson-McGugan, 1976). A conspicuous chert breccio-conglomerate occurs below the sandstones and cherts of the Mowitch and Ranger Canyon formations in the Ganoid Range. It represents the basal part of the Lower Permian Belcourt Formation and is a useful marker bed for helping to locate the boundary between Triassic and older rocks (Fig. 7B). Above and below the Belcourt Formation are unconformities and in the Ganoid Range all of the Belcourt except the basal conglomerate appears to be missing (McGugan and Rapson-McGugan, 1976).

These Permian rocks, which make up the Ishbel Group, lie unconformably on the Mississippian Rundle Group, which

consists of dark grey, fossiliferous limestones and pale grey to white, porous, dolomitic limestones (McGugan and Rapson-McGugan, 1976).

The contact between the Vega-Phroso Siltstone Member and the overlying Whistler Member is generally conformable and distinct. It is placed where the resistant, brownish-grey to rusty-brown weathering siltstones of the Vega-Phroso Member contrast abruptly with the recessive, dark grey-weathering siltstones and limestones of the Whistler Member (Fig. 7A). At many localities the lower 30 cm of the Whistler Member is a phosphatic pebble conglomerate and phosphatic sandstone (Gibson, 1972).

According to Schaeffer and Mangus (1976), the concentration of fossil fish material in the Vega-Phroso Siltstone Member occurs in the upper part of the recessive, thickly laminated, black siltones and shales and continues into the more resistant, blocky siltstones. The fish remains extend through a vertical range of about 10 m but nearly 90 percent of the specimens in situ were found in the lower 1.5 m of the section (Schaeffer and Mangus, 1976). Gibson (1972) reported fish remains at 50 to 65 m above the Triassic-Permian contact on his Mount Becker section and found unidentified vertebrate bone at approximately 115 m. In his Ganoid Ridge section, he found ganoid fish remains at about 55 m (Gibson, personal communication, 1985).

It is difficult to determine exactly where the fish occur stratigraphically because of the great degree of

deformation of the strata, but it was possible to record exact locations for some specimens. On R cirque Allan Lindoe from the University of Alberta located a rich fossil layer in a thin platy, silty shale about 30 to 40 m above the contact between the Vega-Phroso Siltstone Member and the Permian rocks. A more concretionary layer, containing three-dimensional fish and ammonite remains, occurs about 30 m further up section at site X. A layer of resistant siltstone and silty limestone containing coprolites, fish bones and spines of the chondrichthyan "Listracanthus", also occurs further up section from the rich fish bed in R cirque. In F cirque a rich fossil concentration was found at approximately the same level that was reported in Schaeffer and Mangus (1976) from this cirque. Here the fish occur mainly in a massive, blocky siltstone layer. The quarry of Korite Minerals, Ltd., in C cirque is located about the same distance from the Triassic-Permian contact and again occurs over approximately 10 m of beds. As before, a somewhat blocky, more massive siltstone contains much of the material. In D cirque I found a good concentration of bone and partial specimens at about the same level.

It seems that the level of the fish concentrations varies from about 30 to 70 m above the Triassic-Permian contact and may extend over as much as 10 m within any single section. The fish generally occur in a calcareous quartzose siltstone that is dark grey and weathers dark

grey to grey-brown. These beds are up to 25 cm thick, weather shaly to flaggy, and are resistant to slightly recessive. Occasionally the rocks are so calcareous that they may be classed as silty limestones. Additional concentrations of concretionary beds, containing three-dimensional fish fragments in limestone concretions, occur in a siltstone bed at about 115 m above the contact between the Triassic and Paleozoic rocks. A silty limestone layer bearing "Listracanthus" spines, coprolites and isolated fish bones occurs just below this concretionary layer. Unfortunately, no attempt has been made so far to quarry intact strata that have not been overturned or deformed, to locate exactly where the beds occur that bear fossil fishes. More accurate data on the location of these beds must await this type of study.

Invertebrate material collected in situ from above the main fish zone at locality 1 of Schaeffer and Mangus (1976) (F cirque of this paper) was identified by E.T. Tozer of the Geological Survey of Canada. According to him (in Scaeffer and Mangus, 1976) the pelecypod Pseudomonotis occidentalis is the best age indicator and suggests an upper Smithian age. Gibson (1972) collected specimens of the pelecypod Posidonia mimer and the ammonoid Xenoceltites sp. from the same beds that contain fish fragments and indicated that they came from the Euflemingites romunderi Zone, which is lower Smithian in age (Tozer, 1967). Invertebrates collected by the author and the University of Alberta parties also fall

mainly into the Euflemingites romunderi zone. Both Gibson (1972) and Schaeffer and Mangus (1976) agree that the age of these rocks is Smithian but a more precise age for them has not yet been clearly established.

4. Systematic Paleontology

Subclass Actinopterygii

Infraclass Chondrostei (sensu Patterson, 1973)

Order Perleidiformes Berg, 1940

Family Perleididae Brough, 1931

Age Range.- Early to Late Triassic.

Genera assigned.- Andalusias Sykes and Simon, 1979; Boreichthys Selezneva, 1982; Chrotichthys Wade, 1940; Colobodus Agassiz, 1844; Crenilepis Dames, 1888; Dipteronotus Egerton, 1854; Dollopterus Abel, 1906; Manlietta Wade, 1935; Meidiichthys Brough, 1931; Mendocinia Bordas, 1944; Meridensia Andersson, 1916; Nephrotus Meyer, 1851; Perleidus de Alessandri, 1910; Plesioperleidus Su and Li, 1983; Praesemionotus Jorg, 1969; Pristosomus Woodward, 1890; Procheirichthys Wade, 1935; Pseudobeaconia Bordas, 1944; Tripelta Wade, 1940; Zeuchthiscus Wade, 1940.

Diagnosis.- Original diagnoses for the family Perleididae (Brough, 1931; Stensio, 1932) were based mainly on features seen in the genus Perleidus and included characters that were not known for other genera. The following diagnosis taken from Schaeffer (1955) is more appropriate for most members of the family.

> "Body elegantly to deeply fusiform. Snout with nasals separated by postrostral bone, or nasals meeting and postrostral absent. Paired premaxillaries and rostral present. Maxillary with

concave dorsal border, expanded posteriorly, and attached to preopercular. Nasals forming anterior margin of orbit; antorbital absent. Preopercular wedge-shaped, or constricted behind maxillary. Suspensorium moderately oblique to vertical. Suborbital, "supraspiracular", and dermohyal (antopercular) bones may be present or absent. Opercular and subopercular subequal. Interopercular absent. Branchiostegals present. Mandible without coronoid process. Low, rounded teeth on pterygoids (Perleidus, ?Colobodus) and on prearticular (Perleidus, Mendocinia, Colobodus). Basal and fringing fulcra on fins variously developed, possibly absent in a few genera. Fin rays segmented in distal portion only, except in caudal where rays of some genera are completely segmented. Rays of dorsal and anal equal in number to radials. Caudal fin scarcely to moderately forked, hemiheterocercal. Scales and dermal bones smooth, or with ornamentation. Scale structure approaching lepisosteoid type, cosmine layer reduced (Perleidus)."

Discussion.- Hutchinson (1973) agreed with this diagnosis but doubted the absence of antorbitals in perleidids, and described them in Meidiichthys and Manlietta. Antorbitals are also present in Perleidus (Patterson, 1975). The presence of these bones in the

Perleidus from Wapiti Lake is uncertain, as this area is poorly preserved in the material studied.

The correct name that should be employed for the family that includes the genus Perleidus is the subject of an ongoing controversy. When Perleidus was first described by De Alessandri (1910), it was included in the family Catopteridae. Stolley (1920) questioned this assignment, but Stensio (1921) expressed the opinion that Perleidus and all genera then assigned to the Colobodontidae should be placed in the family Catopteridae.

Brough (1931) finally separated the Colobodontidae and the Catopteridae, placing Perleidus, Colobodus and several other genera together in one family. He rejected the name Colobodontidae, which had originally been used by Andersson (1916), because the taxonomic position of Colobodus was uncertain. "A more immediate reason for its rejection lies in the fact that the genus Colobodus must be a member of the Colobodontidae, and at the moment it is very doubtful as to where Colobodus really belongs" (Brough, 1931). Stensio (1932) agreed with Brough's suggestion that the name Perleididae should be used in place of Colobodontidae.

This position was again reviewed by Schaeffer (1967), who pointed out that the type species of Colobodus (C. hogardi) was based on a jaw fragment of uncertain affinity.

The family name Perleididae was in general use from

the time of its inception in 1931 until the mid 1960's. At this time the name Colobodontidae again appeared (Obruchev, 1967; Gardiner, 1967). Both these authors have used the name Perleididae in other publications, however. Since these two publications, both Perleididae and Colobodontidae have been used with about equal frequency.

I agree with Brough (1931) and Schaeffer (1967) and suggest that because of the uncertainty of the taxonomic position of the genus Colobodus, the name Perleididae is the correct name for this family, with the well-known genus Perleidus as its type genus.

Genus Perleidus de Alessandri, 1910.

1889 Semionotus (in part) Deecke, p. 120

1910 Perleidus de Alessandri, p. 49.

1912 Colobodus (in part) Woodward, p. 296.

Type species.- Perleidus altolepis (Deecke, 1889) from the Triassic of Italy.

Other species in the genus.- Perleidus giganteus Beltan, 1972; P. lutoensis Teixeira, 1958; P. madagascariensis Piveteau, 1934; P. piveteaui Lehman, 1952; P. stoschiensis Stensio, 1932; P. viai Beltan, 1972; P. woodwardi Stensio, 1921; P. yangtzensis Su, 1981.

Distribution.- Lower Triassic of Madagascar, Siberia, China, East Greenland, Spitzbergen, and Canada;

Triassic of Italy and Angola.

Diagnosis.- Fishes of small to moderate size, more or less deeply fusiform. Endocranium well ossified, its roof containing only one large fontanelle, which extends through the middle and anterior parts of the otic region. Fossa Bridgei long and clearly defined. Articular fossa for hyomandibular oblique. Vestibular fontanelle not developed. Parasphenoid extending posteriorly to the beginning of the aortic canal (middle of the occipital region). Dermal bones of the skull roof developed according to the palaeoniscid pattern. Parietal square. Intertemporal coalesced with supratemporal. Two to five broad supraorbitals. Hyomandibular inclined somewhat anteriorly so that its dorsal border extends farther anteriorly than its ventral border. Maxilla with low suborbital and high, triangular postorbital parts. Preopercle large with broad dorsal limb; vertical or somewhat inclined anteriorly. Subopercle approximately as high as or higher than opercle. Branchiostegals present but not numerous. Dermal bones of skull ornamented with flat tubercles or ridges of ganoine. Teeth of two kinds (pointed anteriorly and blunt posteriorly) in some species. Anterior teeth with enamel cap in some forms. Fins rather small. Lepidotrichia of caudal fin finely segmented to their base; lepidotrichia of all other fins unsegmented for a long distance proximally. Pelvic fin with few lepidotrichia. Dorsal fin situated rather far posteriorly, opposite either pelvic fins or anterior part

of anal fin. Scales deeper than long on anterolateral part of trunk, decreasing in depth posteriorly, dorsally, and ventrally; rhombic, becoming much longer than deep on the ventral surface of abdominal region. Anterior overlapped area of scales narrow; exposed area with almost-smooth covering of ganoine. Peg-and-socket articulation of scales well developed. In many cases, posterior margin of scales serrated, at least in ventral part. Dorsal ridge scales broader than long, obtuse posteriorly. Dorsal lateral line usually developed (Stensio, 1932).

Perleidus canadensis sp. nov.

Figs. 8, 9, 10.

Etymology.- Named for the country from which it is described.

Holotype.- Complete specimen UAVP 19119, part and counterpart. Collected from the Lower Triassic of Wapiti Lake area, British Columbia, Canada by 1983 University of Alberta field party.

Type locality.- F cirque, Ganoid Range, British Columbia, 54°32'N, 140°45.4'W.

Distribution.- Lower Triassic of western Canada.

Referred specimens.- UAVP (27 specimens) 1310, 1317, 1319, 18988, 18991, 19015, 19059, 19071, 19094, 19100, 19110, 19120, 19122, 22539, 22540, 22541, 22542, 22543, 22544, 22545, 22546, 22547, 22548, 22549, 22550, 22551, 22552, TMP (30 specimens) 83.205.61, 83.205.64,

83.205.65, 83.205.68, 83.205.69, 83.205.70, 83.205.72, 83.205.74, 83.205.76, 83.205.77, 83.205.78, 83.205.79, 83.205.81, 83.205.83, 83.205.85, 83.205.86, 83.205.87, 83.205.88, 83.205.89, 83.205.90, 83.205.91, 83.206.85, 83.206.87, 83.206.88, 83.206.91, 83.206.94, 83.206.97, 83.206.101, 83.206.103, 84.42.19, NMC (14 specimens) 9960, 9982, 10104, 10105, 10106, 10107, 10108, 10109, 12333, 12334, 12335, 12336, 12337, 26215, AMNH (8 specimens) 6266, 6267, 6268, 6269, 6270, 6271, 6272, 6273.

Diagnosis.- Small Perleidus; length of postorbital expansion of maxilla equal to about one half of total length of maxilla. Ventral border of maxilla convex downward for first two-thirds of its length; straight, angling posteroventrally following an inflection in the bone. Anterior margin of preopercle not formed into point along dorsal border of maxilla. Posterior border of subopercle twice as high as anterior border; suture between opercle and subopercle somewhat s-shaped.

Dentition weak in relation to size of fish. Teeth pointed for entire length of both jaws, somewhat smaller posteriorly. Origins of pelvic and dorsal fins far forward. Posterior margins of anterior lateral scales highly serrated.

Description.- A small Perleidus ranging in size from 50 to 70 mm. The maximum depth of the fish occurs behind the pectoral region and is approximately 12.5 to 20 mm (Fig. 8A).

Neurocranium.- The neurocranium is not preserved.

Skull roof.- The skull roof is incompletely known but some of its structure can be seen in several specimens (Fig. 8B). The frontal is large and typical of the genus. It is most similar in relative size and shape to that seen in P. madagascariensis (Fig. 9; Piveteau, 1934). The suture between the frontals appears to have a notch near its center as in the other species of Perleidus (Piveteau, 1934; Stensio, 1932). The greatest width of the frontal is just over the posterior border of the orbit, where a small corner projects (Fig. 9A).

The dermopterotic is fairly long and narrow and connects with the frontal and parietal medially, but its exact shape is difficult to determine. The dermosphenotic is triangular with a long point facing anteriorly (Fig. 9). This is unlike the shape of this bone in any of the other known species of Perleidus and may include the most posterior supraorbital. The exact shape and number of supraorbital bones cannot be determined and it is uncertain whether spiracular plates are present.

The anterior border of the orbit is formed by the nasal, which contains the supraorbital canal (Fig. 9), continuing from the frontal. The exact shape of the nasal cannot be determined, but it is highly curved giving the fish a very blunt snout (Fig. 9). Between the nasals is an unpaired postrostral (Fig. 8B), which articulates with the

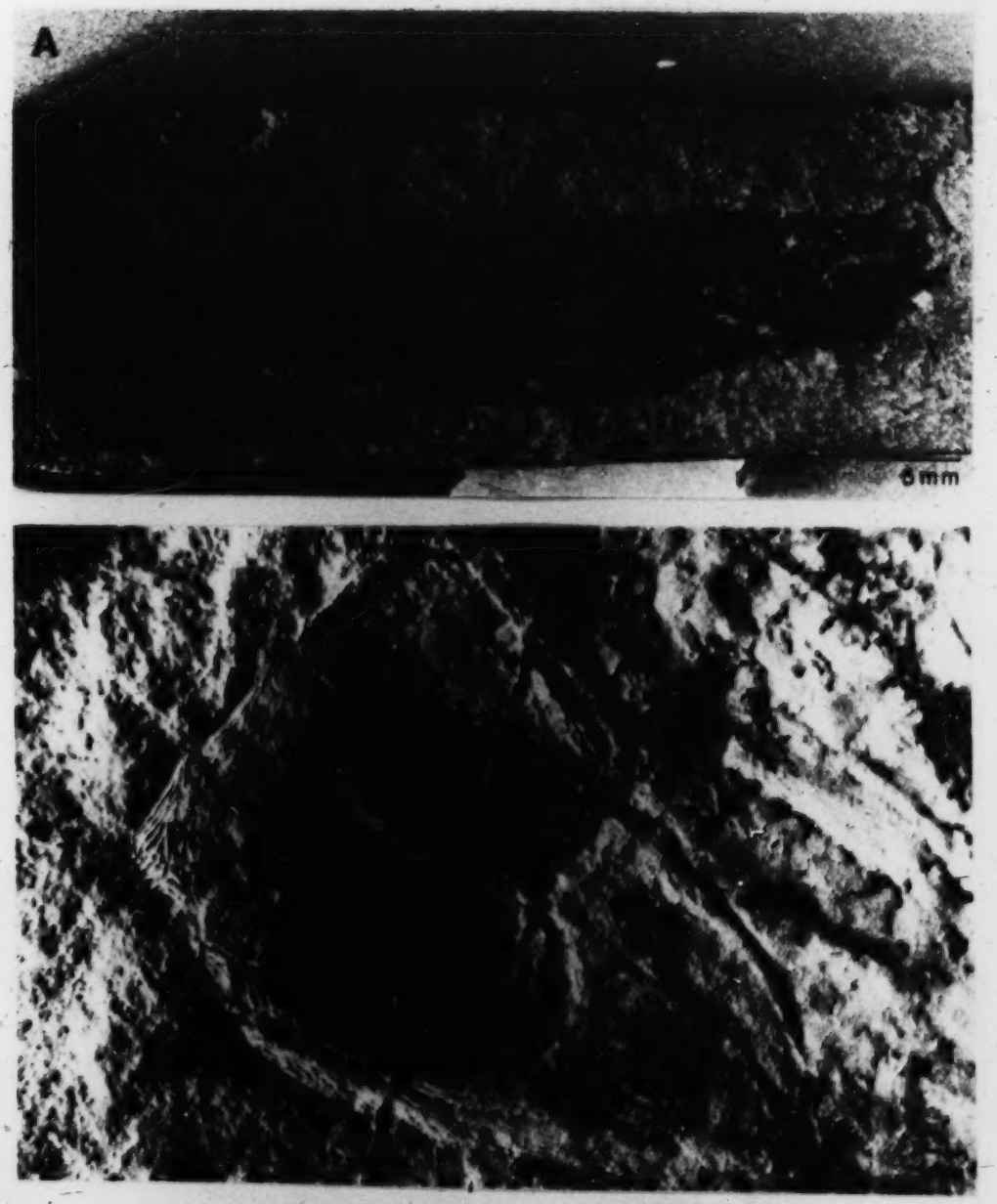

Fig. 8: Perleidus canadensis sp. nov.
A. Complete specimen UAVP 19094.
B. Smooth-On peel of skull roof of TMP 83.206.88.
(Abbreviations are listed on p. xiv).

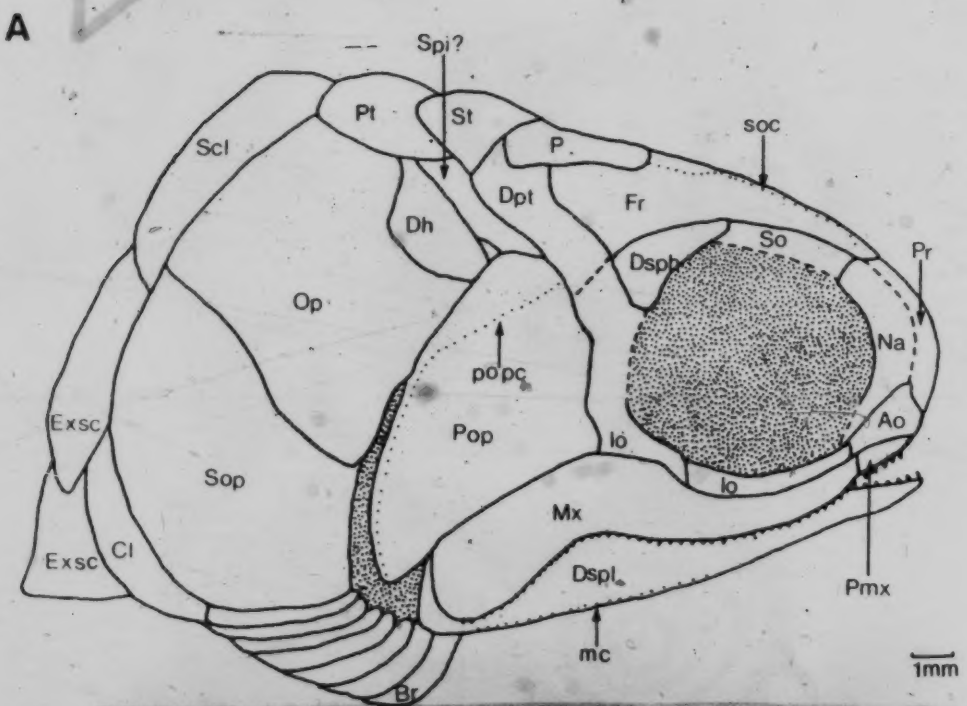

Fig. 9: Perleidus canadensis sp. nov.
A. Composite drawing of the skull based mainly on UAVP 19119.
B. Smooth-On peel of the skull of UAVP 19119 (holotype).
(Abbreviations are listed on p. xiv).

frontals posteriorly, the nasals laterally, and a small rostral anteriorly. The rostral occurs in front of the infraorbital series. All of the bones of the skull roof are ornamented with irregular ridges and tubercles.

The bones of the infraorbital series are imperfectly preserved. A long slender infraorbital is present that has a high posterior portion at the anterior edge of the preopercle and a long slender projection that runs under the orbit to the anterior part of the maxilla (Fig. 9). Other infraorbitals are present, but their exact shapes and relationships are uncertain.

Upper jaw.- The gape is long and reaches to a level well behind the orbit. The premaxilla is distinct and bears teeth (Fig. 9). The shape of the maxilla is generally like that seen in the other species of Perleidus. The posterior part of the maxilla is well developed, reaches back to the preopercle and is firmly connected to it. Beneath the orbit, the maxilla is narrow and curved. The distance between the posterior extremity of the maxilla, and the anterodorsal point that connects with the preopercle, is one half the total length of the bone. The ventral toothed border of the maxilla is highly convex downward for the first two-thirds of its length, then, following an inflection in the margin, it is straight to the posterior margin of the maxilla.

Lower jaw.- The lower jaw is long and low and does not have a coronoid process. It is composed of one

ossification externally, the dentosplenial, which bears the mandibular canal. There is also a small short angular posteriorly. A fairly large bone can be seen internally in several specimens (Fig. 10). It may be the prearticular as Lehman (1952) figured for P. madagascariensis, but it does not appear to be toothed as in the latter species. No remains of the hyomandibular have been recognized.

Opercular series.- The preopercle is large and has a broad dorsal limb and narrow ventral limb (Fig. 9). The anterior margin of the preopercle is convex causing the maximum length of the bone to be approximately one-half the way along its height. This margin does not project forward over the top of the maxilla in a point, but is blunt and rounded. The posterior margin is also convex and long. The anteroventral margin is straight and is in contact with the maxilla. The ventral margin of the preopercle is pointed.

The opercle is large. Its anterodorsal margin is notched for the insertion of the dermohyal. The length of the opercle is approximately equal to its height. Its posteroventral margin is concave anteriorly, then convex. This forms a somewhat s-shaped border with the subopercle. The anteroventral border of the opercle is straight.

The subopercle is about equal in height to the opercle. It is very high on its posterior margin. The posterodorsal tip of the subopercle is rounded. The posterior and ventral borders are convex and the anterior border is slightly concave or straight. A small point is

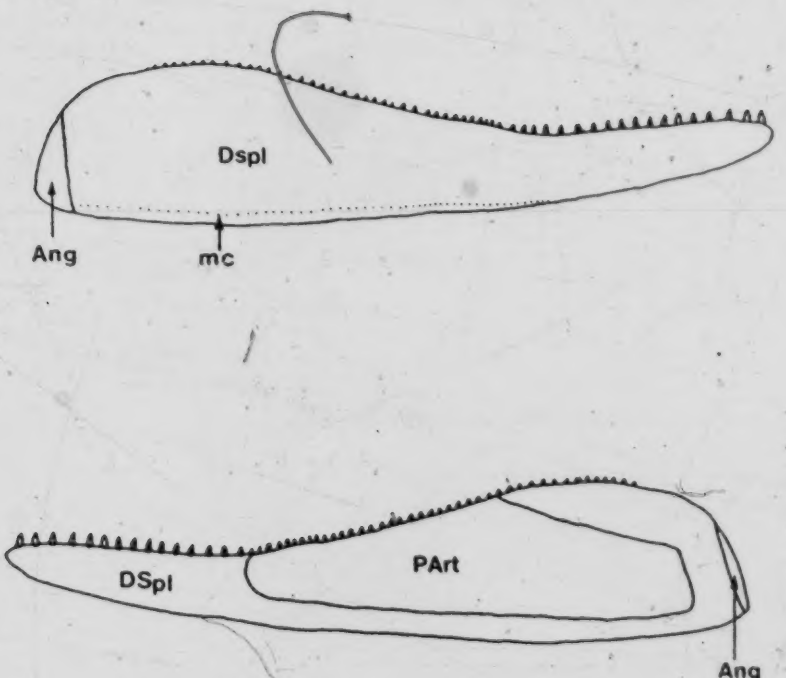

Fig. 10: Right lower jaw of Perleidus canadensis sp. nov.
A. Lateral view (TMP 83.205.85).
B. Medial view (UAVP 19119).
(Abbreviations are listed on p. xiv).

formed antero-dorsally, where it meets the opercle. The branchiostegals are broad. Bones of the cheek and jaws are ornamented in much the same way as the bones of the skull roof.

Dentition.- The dentition is weak in relation to the size of the fish. The teeth are very pointed and may have a small enamel cap, although they are so small and fragile that it is difficult to be sure. The teeth farther back in the jaws are pointed as well although slightly smaller than the anterior ones. The shape of the teeth is consistent for the entire length of the jaws. Teeth on the upper jaws are similar to those on the lower jaws.

Sensory canals.- The supraorbital canal follows the basic pattern seen in other members of the genus as it passes through the frontals. Further trace of this canal and the infraorbital canal has not been recognized. The preopercular and mandibular canals are typical for the genus.

Girdles and paired fins.- The posttemporal, supracleithrum and cleithrum are present and well developed. The clavicle has not been recognized. Two extrascapulars are present (Fig. 9). The dorsal one is long and slender and the ventral one is triangular.

The pectoral fins are well developed but small. They consist of about 10 lepidotrichia that are unsegmented and unbranched proximally, but segmented and branched distally. The pelvic fins originate at about scale row 11

and are closer to the anal fin than to the pectoral fins. The number of lepidotrichia could not be determined.

Median fins.- The dorsal fin is situated far back on the body, originates at about scale row 17 or 18 and is closer to the pelvic fins than to the anal fin. There are about 11 or 12 lepidotrichia. The anal fin has about 11 rays and originates at approximately scale row 18.

The caudal fin is hemiheterocercal and is made up of about 31 lepidotrichia that are segmented. Fulcral scales are present.

Squamation.- The scales are thick and heavy. There are about 39 rows at the level of the lateral line. Scales on the anterolateral part of the body are deeper than long. They decrease in depth ventrally and posteriorly so that posterior scales are rhombic, and those on the ventral surface of the body are longer than deep. The posterior margins, especially in the anterolateral scales, are highly serrated.

Lateral lines of the trunk.- The main lateral line is present but there is no indication of a dorsal lateral line.

Discussion.- This perleidid from western Canada is a fairly typical member of the genus Perleidus with respect to many of its features including the general pattern of the dermal skull roof, cheek, jaws, fins and scales.

The states of some of its characters closely resemble those seen in other species in the genus. Many of

the resemblances are to P. madagascariensis. For example, the ratio of the length of the postorbital expansion of the maxilla to the total length of the maxilla is similar to this ratio in P. madagascariensis, as is the general shape of the preopercle. The dentition is somewhat like that seen in P. madagascariensis but is much weaker than in any other species. The dorsal margins of the anterior lateral scales are highly serrated, also like the condition seen in P. madagascariensis.

Other combinations of characters more closely resemble those seen in other species of the genus Perleidus. The shape of the preopercle is very similar to that seen in P. yangtzensis. The posterior margin of the subopercle is very high as in P. stoschiensis but the posterodorsal tip of the subopercle is more rounded than in that species. The origin of the dorsal fin is far forward as in P. altolepis. The position of the pelvic fins is most similar to the position of these fins in P. woodwardi, and the serrations on the posterior margin of the scales in P. canadensis resemble those seen in P. woodwardi even more than P. madagascariensis.

In still other respects, the species described here is not like any of the known species of Perleidus. The ventral, toothed border of the maxilla is straight in most members of the genus Perleidus, but in the Canadian Perleidus it is highly convex downward for the first two-thirds of its length. The dentition is much weaker

than in any of the other species of Perleidus and consists of only sharply pointed teeth. In most other members of the genus, there are two types of teeth, pointed and blunt. The origins of the dorsal and pelvic fins are farther forward than in any of the other species in the genus.

Taking into account the unique combination of characters described above, it is necessary to erect a new species for the Canadian material.

cf. Perleidus sp.

Schaeffer and Mangus (1976) reported a second perleidid from Wapiti Lake that they tentatively referred to the genus Perleidus. They also pointed out several similarities between this animal and Meridensia. Unfortunately no new material of this species has been found, and the two original specimens are not well enough preserved for identification.

These two specimens (AMNH 6265 and NMC 12323) are much larger than Perleidus canadensis and reach lengths of up to 30 cm. They clearly show an ovoid postorbital expansion of the maxilla that is fixed to the preopercle, a mandible without a coronoid process and large blunt teeth of the perleidid type. There is no evidence for an interopercle, a supramaxilla or an ethmoid process on the maxilla. Generic identification of these specimens must await collection of more nearly complete material.

Infraclass Neopterygii (*sensu* Patterson, 1973)

Order Parasemionotiformes Lehman, 1966

Family Parasemionotidae Stensio, 1932

Remarks.- A discussion of the classification of this group is given in the chapter titled Discussion of Phylogeny.

Genus *Watsonulus* Brough, 1939

1934 *Watsonia* Piveteau, p. 137.

1939 *Watsonulus* Brough, p. 91.

Type species.- *Watsonulus eugnathoides* (Piveteau, 1934) from the Early Triassic of Madagascar.

Age Range.- Early Triassic.

Distribution.- Lower Triassic of Madagascar, East Greenland and Canada.

Diagnosis.- Moderately deep-bodied parasemionotid with relatively long, low skull. Dorsal limb of preopercle broad and unfragmented. Maxilla long, reaching to anterior border of preopercle.

Discussion.- *Watsonulus* differs from most other genera in the family Parasemionotidae by its wide, unfragmented preopercle, by the absence of suborbitals, and by the structure of the neurocranium. It is most similar to *Parasemionotus*, *Ospia* and *Broughia*.

Watsonulus differs from *Parasemionotus* mainly by its wider, unfragmented preopercle that is inclined

slightly forward. In Parasemionotus the preopercle is relatively narrow and is either vertical or inclined slightly posteriorly. There are usually several suborbitals present on the anterodorsal margin of the preopercle that are probably formed by the fragmentation of the anterior rim of the preopercle (Gardiner, 1967). The angle between the horizontal and vertical pit lines on the anterior portion of the preopercle is more acute in Watsonulus than in Parasemionotus (Stensio, 1947; Lehman, 1952).

Additional differences between Watsonulus and Parasemionotus are in the shape of the gular plate and in the structure of the neurocranium. The maxilla is longer in Watsonulus and the gular plate is wider and more oblong in shape (Lehman, 1952, fig. 122). On the neurocranium, the hyomandibular facet is longer in Watsonulus and the postorbital process is much less pronounced (Lehman, 1952).

Watsonulus differs from Ospia by the greater width of the preopercle, especially along its dorsal and ventral borders (Stensio, 1932, p. 260), by the greater size of the subopercle, by its more pointed teeth (in Ospia the teeth are blunt) and by features of the neurocranium. On the neurocranium, the hyomandibular facet is wider in Watsonulus, the occipital region is longer, the jugular depression is less marked and the glossopharyngeal opening is located more posteriorly. The vestibular fontanelle is present in Watsonulus, absent

in Ospia. There is only one fossa Bridgei in Watsonulus, two in Ospia. In Watsonulus the facial and trigeminal nerves have a common opening and the optic fenestra is larger (Lehman, 1952).

Finally, Watsonulus differs from Broughia by its broader preopercle (although the preopercle in Broughia is poorly known), by its longer, shallower maxilla, smaller, more numerous teeth, longer dorsal and anal fins and by its serrated scales (Stensio, 1932). There are also differences in the neurocrania, which include a longer occipital region in Watsonulus, a less curved hyomandibular facet, a less pronounced postorbital process and the structure of the aortic canal. In Broughia, a short aortic canal runs below the posterior end of the neurocranium whereas in Watsonulus there is only an open groove there (Lehman, 1952).

Watsonulus eugnathoides (Piveteau, 1934)

Discussion.- Watsonulus eugnathoides was first described from the Ankitohazo Basin of northeastern Madagascar as Watsonia eugnathoides by Piveteau (1934). Brough (1939) pointed out that the generic name Watsonia was preoccupied at least three times and re-named this genus Watsonulus.

Piveteau's original work on W. eugnathoides included three different morphs that he called Type A,

Type B and Type C. He noted that the three forms differed in the depth of the body, in the structure of the preopercle and in ornamentation of the scales. He suggested that the differences in the preopercles were probably related to the dimensions of the individuals and the differences in the scales were probably due to conditions of preservation. He therefore identified the three forms, which he claimed were remarkably homogeneous in their basic characters, as belonging to one species (Piveteau, 1934).

Piveteau (1939-40) supplemented his work on the skull roof of Watsonulus eugnathoides by reference to another specimen from the Ankitohazo basin that he stated was most similar to his Type A. Lehman (1952) was the first to describe the neurocranium of W. eugnathoides and commented on other features of the skull. His work involved a review of specimens in l'Ecole des Mines de Paris, the British Museum of Natural History and the Musee National d'Histoire Naturelle de Paris. The specimens studied all came from northeastern Madagascar.

Lehman (1952) also commented on the variation evident in the specimens that he reviewed but noted that scale counts were consistent with those of Watsonulus eugnathoides. He did not see any of Piveteau's Type A specimens but did see his Type B and C, which formed Lehman's Type 1. These forms had preopercles with narrow ventral limbs and were ornamented with long striations and tubercles (Lehman, 1952, fig. 109). He also discussed two

other forms not seen by Piveteau. The first of these had a preopercle with a narrow ventral limb but also had a projecting lobe in this area (Lehman, 1952, fig. 106). The ornamentation was also very different in this form. His Type 3 was completely unornamented and had a very large opercle and subopercle (Lehman, 1952, fig. 107). Lehman admitted that it was possible to distinguish several varieties of Watsonulus eugnathoides but that it was difficult to determine whether these different forms represented distinct species.

Lehman, et al. (1959) studied additional parasemionotids from Antanamary in southwestern Madagascar. There were several differences in the structure and meristic characters between these specimens and the ones from northeastern Madagascar, but the authors concluded that these specimens were also members of the species W. eugnathoides. They did mention, however, that work on additional material was necessary in order to establish whether W. eugnathoides was in fact a homogeneous species. Lehman (1966) said that this species is probably heterogeneus and that there is considerable difference in the size of the preopercle among the specimens that have been assigned to the species W. eugnathoides.

Further contributions to the description of Watsonulus were made by Beltan (1968) and Olsen (1984).

I believe that the material so far included in the

species Watsonulus eugnathoides actually represents more than one taxon. Scale counts taken from photographs of Piveteau's original material show different numbers of scale rows present in the three forms. Piveteau's Type A has 40 scale rows, which is comparable to the number found in the Wapiti Lake Watsonulus. His Type B has 50 scale rows and his Type C has 34. Unfortunately, Lehman did not publish the number of scale rows seen in his three morphs.

There is also significant variation in the relationships of some of the bones of the skull, especially the size and shape of the preopercle, in the various specimens assigned to the species W. eugnathoides. Fig. 11 shows digitized outlines of the preopercles of several parasemionotids, including some of the specimens that have been assigned to W. eugnathoides. When these outlines are superimposed (Fig. 11L) the variation in shape of the preopercle becomes evident.

There has never been a specimen designated as holotype for Watsonulus eugnathoides and the possible syntypes from Piveteau's original publication probably represent more than one species. This, coupled with the assignment of several other forms to the species by Lehman (1952; Lehman, et al., 1959), makes it very difficult to establish an accurate diagnosis for the species. Without an accurate diagnosis, it is difficult to make a comparison between the Canadian parasemionotids and Watsonulus eugnathoides. I believe that a complete

revision of the genus Watsonulus is necessary and hope to have an opportunity to approach this problem in the future.

A summary of meristic and morphometric data is given in Table 1 for some of the specimens from the published literature and for two AMNH specimens assigned to Watsonulus eugnathoides. A complete table of measurements and counts is given in Appendix 1. These tables show the amount of variation that is present in the specimens assigned to this species.

Fig. 11a: Digitized outlines of preopercles from various specimens of Watsonulus eugnathoides, Laudonia and Ospia. Dotted lines represent sensory canals.

A) Ospia whitei, from text fig. 84 (Stensio, 1932). About x3.

B) Laudonia brevicephala, UAVP 22301. About x3.

C) Watsonulus eugnathoides Type 2, from fig. 106 (Lehman, 1952). About x3.

D) W. eugnathoides Type B, from plate VIII, fig. 1 (Piveteau, 1934). About x4.5.

E) W. eugnathoides Type C, from fig. 43 (Piveteau, 1934). About x6.

F) W. eugnathoides, from fig. 1 (Olsen, 1984). About x2.

A
B
C
D
E
F

Fig. 11b: Digitized outlines of preopercles from various specimens of Watsonulus eugnathoides and W. cf. W. eugnathoides. Dotted lines represent sensory canals.

G. Type A, from plate VII, fig. 3 (Piveteau, 1934). About x3.

H. AMNH 11732. About x3.

I. Watsonulus cf. W. eugnathoides, UAVP 22299. About x3.3.

J. Type 1, from fig. 109B (Lehman, 1952). About x6.

K. Type 3, from plate 42, fig. D (Lehman, 1952). About x5.

L. Superimposed outlines of preopercles from specimens of the genus Watsonulus, illustrated separately as C-K (above).

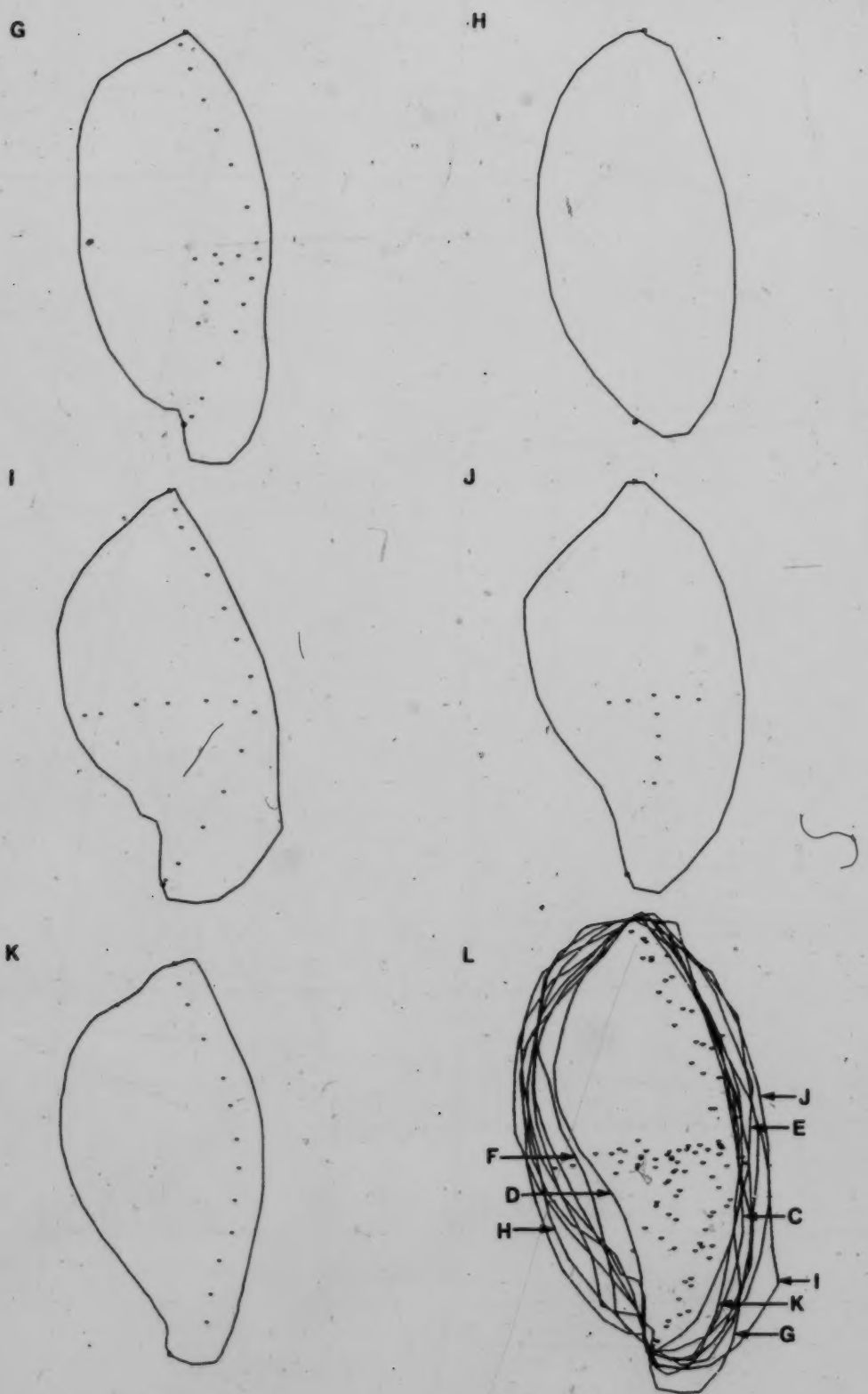
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Table 1

Summary statistics of morphometric and meristic data for *Watsonulus* - Part 1

All proportional measurements presented as means with number of observations and ranges in parentheses. All measurements in mm. Abbreviations are listed on p. 10-12.

	Type A	Type B	Type C	Type 2	Type 3
SL	155	122	85	-	-
HL	38(5; 30-51)	38(1)	30(1)	37(2; 36-37)	36(1)
HL/SL	.29(1)	.31(1)	.35(1)	-	-
HD	29(6; 20-40)	23(1)	19(1)	28(2; 27-29)	22(1)
HD/HL	.70(6; .62-.80)	.61(1)	.63(1)	.78(2; .74-.82)	.61(1)
BD	47(1)	35(1)	-	-	-
BD/SL	.30(1)	.28(1)	-	-	-
MD/ML	.24(4; .17-.27)	.16(1)	-	.23(2; .22-.24)	.61(1)
ML/POPD	.97(5; .92-1.08)	1.15(1)	-	1.10(2; .99-1.21)	1.13(1)
OPL/OPD	<1(5)	>1(1)	=1(1)	<1(2)	>1(1)
OPL/HL	.44(5; .41-.47)	.45(1)	.37(1)	.41(2; .37-.44)	.37(1)
ML/HL	.40(4; .35-.45)	.51(1)	-	.50(2;	.41(1)
TS	40(1)	50(1)	34(1)	-	-
SDF	24-25(2)	29(1)	-	-	-
SAF	18-19(2)	26(1)	-	-	-
P_1F	15(1)	-	-	-	-
P_2F	-	-	-	-	-
DR	15(1)	12(1)	-	-	-
AR	12(1)	11(1)	-	-	-
CR	-	13(1)	13(1)	-	-
PL/SL	-	-	-	-	-

Table 1

Summary statistics of morphometric and meristic data for Watsonulus - Part 2

All proportional measurements presented as means with number of observations and ranges in parentheses. All measurements in mm. Abbreviations are listed on p. 10-12.

	SW Madagascar form	W. cf. W. eugnathoides
SL	-	131(4;80-173)
HL	22(3;22-23)	44(6;28-51)
HL/SL	-	.32(4;.30-.35)
HD	14(3;14-15)	25(6;17-30)
HD/HL	.66(3;.66-.67)	.57(6;.53-.66)
BD	-	273(4;18-36)
BD/SL	-	.21(4;.17-.23)
MD/ML	.28(2;.27-.28)	.19(6;.16-.21)
ML/POPD	.80(2;.78-.82)	1.16(6;1.04-1.28)
OPL/OPD	<1(3)	>1(6)
OPL/HL	.39(3;.38-.41)	.35(6;.29-.41)
ML/HL	.36(2)	.44(6;.41-.48)
TS		39-40(5)
SDF	28(3)	23-25(4)
SAF	24(3)	18-20(4)
P_1F	10(1)	15(2)
P_2F	-	9(1)
DR	15(1)	16-17(2)
AR	-	12-13(2)
CR	-	15(2)
PL/SL	-	.18(4;.14-.21)

Watsonulus cf. W. eugnathoides

Figs. 12, 13.

Referred specimens.- UAVP 19124, 19125, 19126, 19128, 22110, 22299, TMP 84.42.2, UC 1156, NMC 10113. Other specimens tentatively referred to this taxon based mainly on size and head and body shape are UAVP 19092, 19129, 19130, 19132, 19137, 20345, 22297, 22302, 22309, 22553, 22554, TMP 83.206.83, UC 1151, 1152, 1157 NMC 10121 and 26213.

Description.- Specimens from Wapiti Lake referred to Watsonulus cf. W. eugnathoides reach maximum lengths of 130 to 180 mm.

Neurocranium.- The neurocranium is not preserved in any of the specimens studied.

Skull roof.- Paired nasals, frontals, parietals, dermopterotics, supratemporals and posttemporals are present as in other parasemionotids and in holosteans generally (Fig. 12, 13; Piveteau, 1934; Lehman, 1952; Stensio, 1932; Olsen, 1984). All bones of the skull roof are covered with a fine sculpture of tubercles and ridges.

The nasal is large and is narrow posteriorly where it meets the frontal. As it extends anteriorly, it widens, before narrowing again along its anterior margin. The shape of the nasal is much as that seen in the undetermined parasemionotid from East Greenland (Patterson, 1975) and not rectangular as in Watsonulus (Olsen, 1984; Piveteau, 1934). Olsen notes, however,

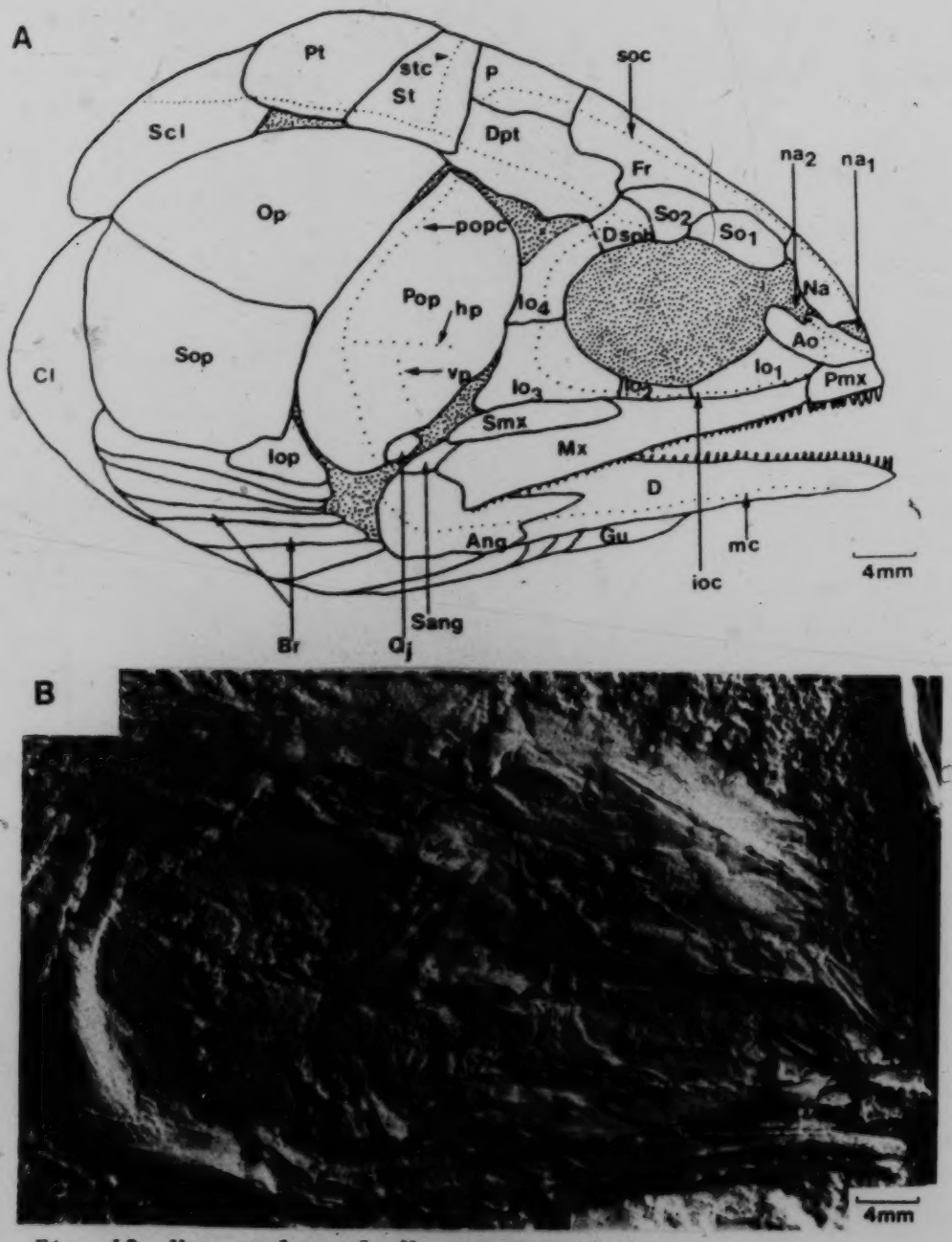


Fig. 12: Watsonulus cf. W. eugnathoides.
A. Composite drawing of the skull based mainly on UAVP 19124 and UAVP 19128.
B. Smooth-On peel of the skull of UAVP 19124.
(Abbreviations are listed on p. xiv).

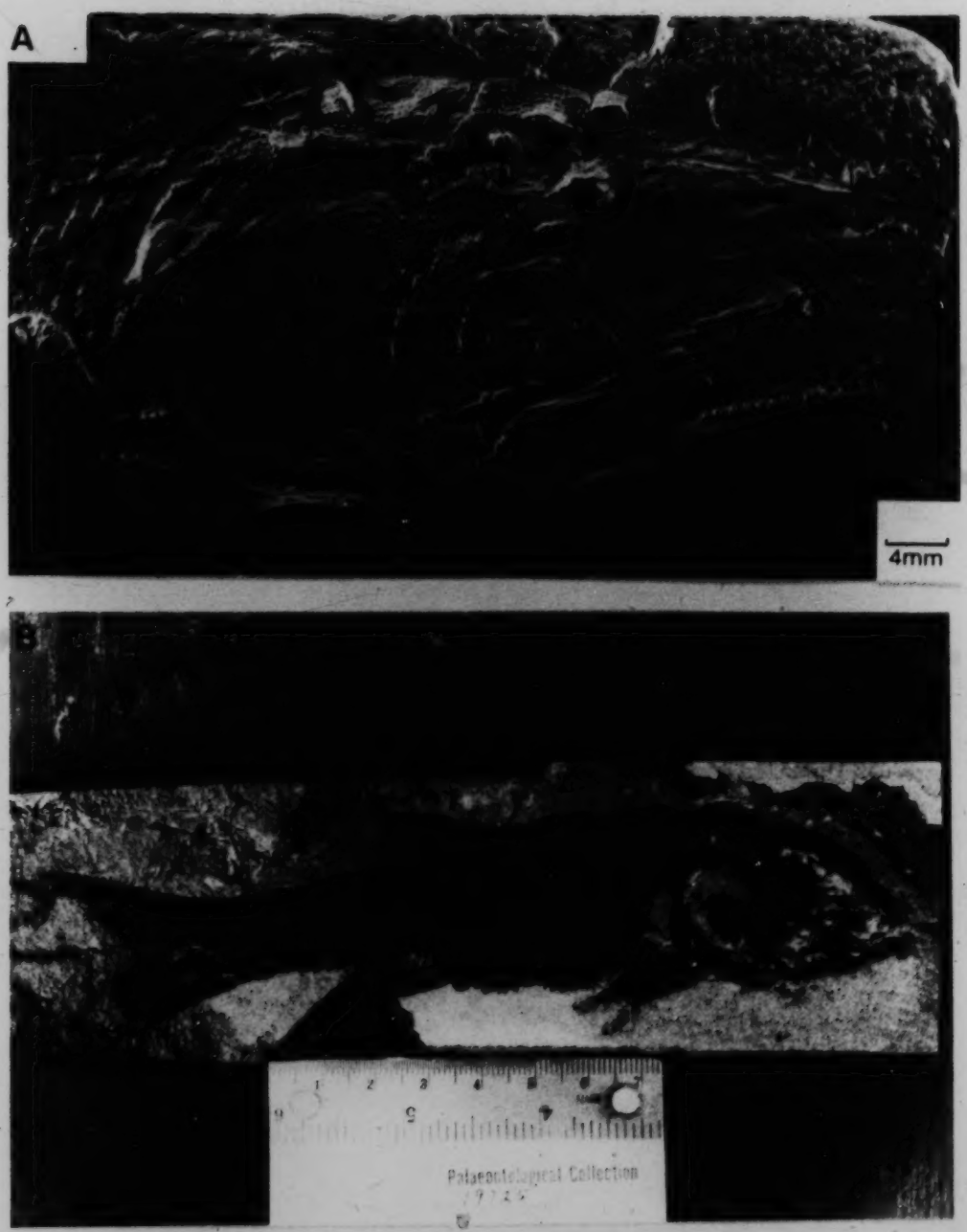


Fig. 13: Watsonulus cf. W. eugnathoides.
A. Smooth-On peel of the skull of UAVP 19128.
B. Complete specimen (UAVP 19125).
(Abbreviations are listed on p. xiv).

that the nasal in some of his specimens is shaped like the nasal in Patterson's parasemionotid. This bone is approximately one-third the length of the frontal. A rostral has not yet been recognized.

The frontal is the largest element of the skull roof and is virtually identical to that described by Olsen (1984) for Watsonulus and by Stensio (1932) for Ospia and Broughia. The width of this bone is about half its length. The parietal is small as in other holosteans. The dermopterotic is almost square but less than half of the medial edge of the bone is in contact with the frontal, unlike the condition in Watsonulus eugnathoides (Lehman, 1952; Olsen, 1984). Anteriorly this bone is in contact with the dermosphenotic and the posterior supraorbital. The supratemporal is of the usual triangular holostean shape.

There are at least four canal-bearing infraorbitals forming the posterior and ventral borders of the orbit (Fig. 12, 13). The first infraorbital (lachrymal) is triangular and is about two-thirds the size of the third. The second is a narrow tube surrounding the infraorbital canal. The third is subtriangular and the shape of the fourth is uncertain owing to poor preservation. The dermosphenotic also bears part of the infraorbital canal but its exact shape is unclear; it is, however, wide and square dorsally.

There are two supraorbitals. The posterior one is

triangular and the anterior one, oval. The anterior one is not very long, so does not curve around the front of the orbit as in fig. 1 of Olsen (1984), and does not contact the first infraorbital (Fig. 12). It comes in contact instead only with the nasal as in fig. 107 of Lehman (1952) and in the undetermined parasemionotid (Patterson, 1975, fig. 137). The antorbital is the same "L-shape" as described by Olsen (1984) and Patterson (1975). On the lateral surface of the antorbital, the infraorbital canal gives off a branch that runs dorsally through this bone. The antorbital forms part of the anterior border of the orbit (Fig. 12).

The first naris occurs between the medial process of the antorbital and the anterior part of the nasal. The second naris occurs just lateral to the posterior part of the nasal (Fig. 12).

Upper jaw.- The premaxilla is separate from the rostral and bears approximately 10 large pointed teeth. The maxilla is long and shallow, and extends almost to the preopercle. The maxilla has a notch on its posteroventral border and a long anteromedial process that articulates with the premaxilla (Olsen, 1984). As Schaeffer and Mangus (1976) suggested, this bone is much like that found in Watsonulus. The length of the maxilla makes up 40 to 48 percent of the total length of the skull. The ratio of the depth of the maxilla to the length of its dentigerous portion is between 0.15 and 0.21.

The teeth on the maxilla are large on the anterior

part of the bone but become progressively smaller posteriorly. There are many teeth as in Watsonulus (Olsen, 1984). The supramaxilla is long and shallow and is slightly less than one-half the length of the toothed portion of the maxilla. These bones are only sparsely ornamented.

Lower jaw.- The lower jaw is long and low and has a high coronoid process. It is of the typical holostean type. The main part of the lower jaw is composed of the dentary laterally, which bears more than 25 sharp teeth. These teeth oppose the larger, more anterior teeth on the maxilla. Posteriorly there is at least an angular and a surangular (Fig. 12, 13A). A typical mandibular sensory canal runs along the ventral border of the lower jaw. The angular and the ventral portion of the dentary are highly sculptured with ridges and tubercles. The surangular, and the area of the dentary covered by the maxilla when the mouth is closed, are smooth. Nothing is known of the medial elements of the jaw.

Opercular series.- The preopercle is similar in shape to the one seen in some of the described specimens of Watsonulus eugnathoides, but differs from others (Fig. 11). This variation in preopercular shape is discussed below. The preopercle is substantially wider than that of Ospia (Stensio, 1932), especially along its dorsal and ventral borders. The horizontal and vertical pit lines form a fairly acute angle, as noted by Lehman (1952) and

Stensio (1947) for Watsonulus eugnathoides.

The posterior border of the preopercle is thickened for the preopercular canal and the anteroventral edge is notched for the quadratojugal. The maxilla is longer than the preopercle is deep.

The opercle is convex on its dorsal and ventral borders. It is longer from its anterior to posterior borders than it is deep. The ratio of the length of the opercle to the length of the skull is between 0.28 and 0.40. The subopercle is approximately the same size as the opercle and has an upturned anterior projection that overlaps the opercle (Fig. 12, 13A). The border between the subopercle and the opercle is convex ventrally for a short distance anteriorly, then is straight. The interopercle is small and triangular. These bones are covered with a sculpture of tubercles and ridges.

Branchiostegals are fairly numerous and the shape of the gular is uncertain.

Hyomandibular.- The hyomandibular is preserved pressed against the medial edge of the preopercle in most specimens, often causing distortion of the latter. It is inclined slightly anteriorly and is basically like the hyomandibular described by Olsen (1984) and Stensio (1932) for other members of the family.

Pectoral girdle.- The cleithrum is of the typical holostean "C-shape" and is covered laterally with ridged sculpture. A clavicle is present that is similar to the one described by Lehman (1952) and Olsen (1984) for

Watsonulus, but its exact size and shape cannot be determined. The supracleithrum and posttemporal are very similar to those in Watsonulus (Fig. 12). These bones are all covered with typical ornament.

Paired fins.- The pectoral fins bear approximately 14 lepidotrichia that are unbranched for about 20 percent of their length. They are short, reaching barely to the origin of the pelvic fins (Fig. 12B). The ratio of the length of the pectoral fins to the standard length of the fish is 0.16 to 0.21. The pelvic fins are small and are slightly closer to the anal fin than to the pectoral fins. The number of lepidotrichia is uncertain.

Median fins.- The dorsal fin originates about half way along the body, slightly in front of the anal (Fig. 12B). It bears approximately five fringing fulcra and 17 or 18 lepidotrichia. The anal fin bears 13 or 14 lepidotrichia but an accurate count on this fin has not been possible. The caudal fin bears about 15 lepidotrichia above the midline. Several large basal fulcra occur in front of the anal, dorsal and caudal fins.

Squamation.- These fishes are covered with typical parasemionotid scales. There are approximately 40 rows of scales between the extracleithral elements and the base of the caudal fin. The anal fin originates between rows 18 and 20 and the dorsal fin between rows 23 and 25.

Additional data on meristic and morphometric characters of these fishes are given in Appendix 1.

Discussion.- As discussed above, it is difficult to make a direct comparison between the specimens from Wapiti Lake and Watsonulus eugnathoides: There has never been a holotype designated for the species W. eugnathoides, the possible syntypes may represent more than one taxon, and significant variation is present in the different specimens assigned to this species. The following comments are based on the descriptions of the different morphs of Watsonulus eugnathoides given in the literature and on the meristic and morphometric data listed in Table 1 and Appendix 1.

There is a resemblance in the shape and relationships of most of the skull bones between Watsonulus from Wapiti Lake and Watsonulus eugnathoides. The ratio of the length of the skull to the standard length is very similar among all the various forms. The shape of the preopercle in the Watsonulus from Wapiti Lake does fall within the range of variation seen in the specimens so far assigned to W. eugnathoides (Fig. 11). In the Watsonulus from Wapiti Lake, this bone is most similar to Piveteau's Type A and Lehman's Type 1 but is not exactly like either one. The ratio of the depth of the maxilla to the length of the maxilla is most similar to Piveteau's Type B and Olsen's specimen YPM 8994. The ratio of the length of the maxilla to the depth of the preopercle is similar to this ratio in Watsonulus eugnathoides and is most similar to that seen in

Piveteau's Type B, Lehman's Type 2 and 3 and Olsen's specimen YPM 8994.

The opercle seen in the Wapiti Lake Watsonulus is longer than deep as in Piveteau's Type B and Lehman's Type 3. The ratio of the length of the opercle to the length of the skull is similar to that seen in Piveteau's Type C, Lehman's Type 2 and Type 3 and two of Lehman, et al.'s specimens from southwestern Madagascar. The ratio of the length of the maxilla to length of the skull is similar to Piveteau's Type A, Lehman's Type 3 and Olsen's YPM 8994.

The total number of rows of scales and the number of rows of scales anterior to the dorsal and anal fins, as well as the dorsal and anal fin-ray counts, are like those seen in Piveteau's Type A and in AMNH 11734.

A number of differences distinguish Watsonulus from western Canada and Watsonulus eugnathoides. The Canadian Watsonulus has a longer, shallower head than most of the other described material in the genus and has a longer, shallower body. Types B and C of Piveteau (1934) differ substantially from the specimens from Canada in number of scale rows, and Watsonulus eugnathoides from southwestern Madagascar shows fin-ray counts different from those in the Canadian Watsonulus.

I believe that Watsonulus from Canada is similar enough to Watsonulus from Madagascar to be placed in the same genus, and is most similar to Piveteau's Type A. It is difficult, however, to refer the Wapiti Lake material

to the species Watsonulus eugnathoides because, although it does resemble some of the described material, it also differs substantially in many respects from other specimens assigned to this species. I therefore assign the Wapiti Lake Watsonulus to Watsonulus cf. W. eugnathoides and suggest that only through a complete revision of the genus Watsonulus can a more definite specific assignment be made.

Genus Laudonia gen. nov.

Type and only species.- Laudonia brevicephala gen. et sp. nov.

Etymology.- After L.A. Laudon, discoverer of the Wapiti Lake sites.

Diagnosis.- Deep bodied parasemionotid of moderate size; head short, deep. Pectoral fins short, reaching only to origin of pelvic fins. Preopercle relatively narrow; entire and unfragmented. Suborbitals lacking in available specimens. Maxilla relatively long and deep.

Discussion.- Laudonia differs from most other parasemionotids by the unfragmented preopercle and the lack of suborbitals. It differs from Watsonulus by the much narrower preopercle (Fig. 11), deeper head and body (Fig. 3), different relationship of the opercle and subopercle, and by the different shape of the gular plate.

The shape of the preopercle in Laudonia resembles that of Ospia but it is wider along its ventral margin and the sensory canal is different, angling across the lower part of the bone rather than following the posterior margin (Fig. 11). The subopercle is larger in relation to the size of the opercle in Laudonia and the border between these two bones is very different.

Laudonia differs from Broughia in the smaller size of the teeth, the shape of the border between the opercle and subopercle and the shapes of some of the bones

of the skull roof. There are also differences in the numbers of lepidotrichia in the dorsal and anal fins. It is difficult to compare Laudonia with Ospia and Broughia because the latter two genera are based largely on the structure of the endocranium and this is not preserved in the Wapiti Lake material. Comparison of the known skull bones among these three genera, however, does show that they are sufficiently different to warrant the designation of a new genus.

Laudonia brevicephala sp. nov.

Figs. 14, 15, 16.

Etymology.- Brevis, Latin, adjective, "short"; cephalus, Greek (kephalos), noun, "having a specified type of head".

Holotype.- UAVP 22308 (Fig. 14 and 15), a complete skull and skeleton in part and counterpart, collected by L.A. Lindoe from the Lower Triassic Sulphur Mountain Formation in eastern British Columbia.

Type locality.- R cirque on the Ganoid Range, near Wapiti Lake, British Columbia (54°32.5'N, 120°45.5'W).

Distribution.- Lower Triassic of western Canada.

Referred specimens.- UAVP 19133, 22112, 22301, 22303, 22304, 22310, TMP 83.206.51 (counterpart UAVP 22300), 83.206.62, 83.206.153 and UC 1191. Other specimens referred mainly on the basis of general size and body proportions are UAVP 19109, 19123, TMP 83.206.35, 83.206.54, 84.42.12 and 85.42.16B.

Diagnosis.- Same as for the genus.

Description.- Specimens of Laudonia brevicephala reach an approximate maximum total length of 125 mm. The head is shorter and deeper than in Watsonulus cf. W. eugnathoides. This is reflected in the shorter jaws, deeper, narrower preopercle and narrower opercle and subopercle. The body is also deeper than in Watsonulus cf. W. eugnathoides, reaching a body depth of approximately 40 mm.

Neurocranium.- The neurocranium is not preserved in available specimens.

Skull roof.- The bones of the skull roof are basically like those in Watsonulus cf. W. eugnathoides and are heavily ornamented with tubercles and ridges. The parietal appears to be somewhat smaller than in W. eugnathoides and the dermopterotic is shorter and deeper (Fig. 14A). The nasal is wider than in Watsonulus cf. W. eugnathoides and is squarish. It is approximately half the length of the frontal. The rostral has not been recognized.

The frontal is typically parasemionotid in size and shape and the parietal is small. The dermopterotic is deep and short with greater than half of its medial border in contact with the frontal. Anteriorly it contacts the dermosphenotic and posterior supraorbital. The supratemporal and posttemporal are of the usual shape except that the supratemporal is short.

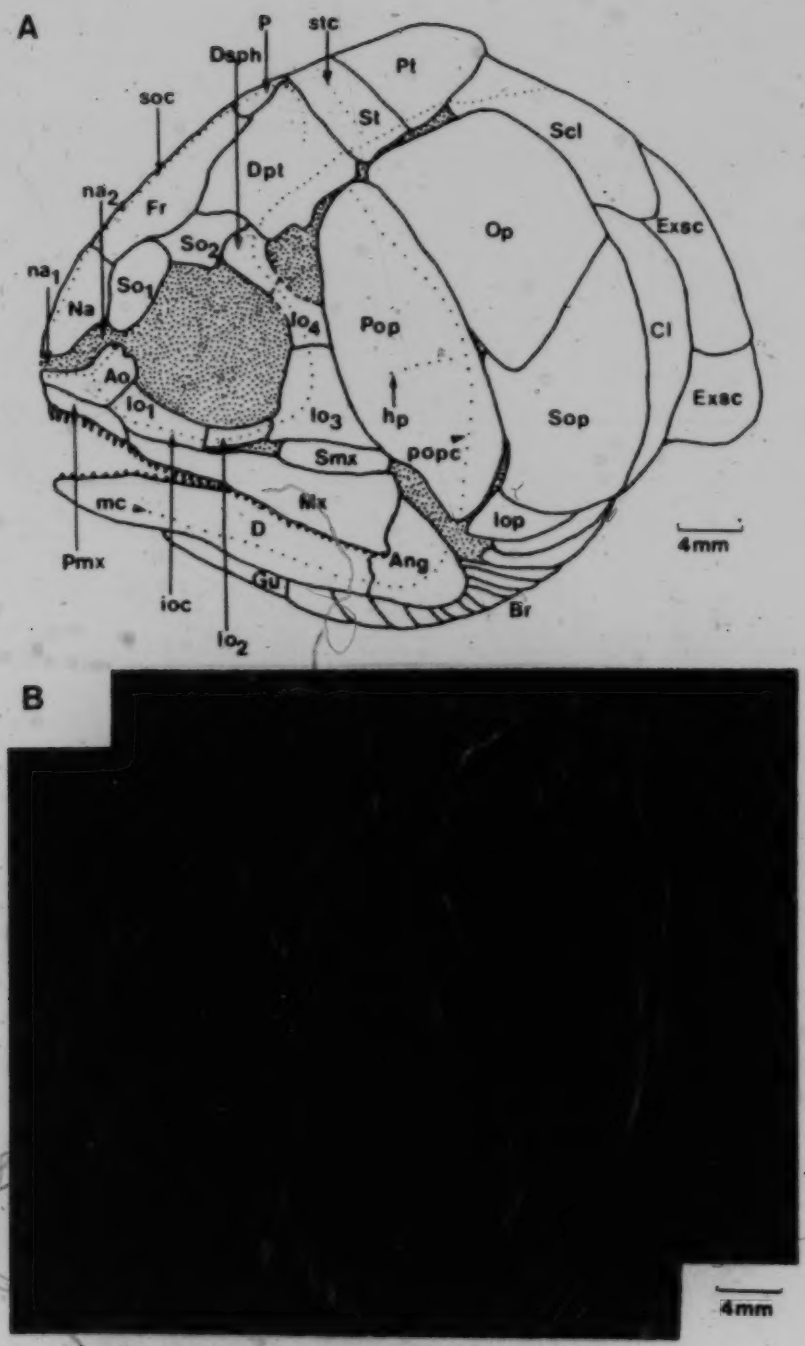


Fig. 14: Laudonia brevicephala gen. et sp. nov.
A. Composite drawing of the skull based on UAVP 22301 and UAVP 22308.
B. Smooth-On peel of UAVP 22308 (holotype).
(Abbreviations are listed on p. xiv).

There are four canal-bearing infraorbitals (Fig. 14A) forming the posterior and ventral borders of the orbit. The rest of the margin of the orbit is formed by the antorbital and first supraorbital anteriorly, the two supraorbitals dorsally, and the dermosphenotic posterodorsally. These bones are shaped basically like those in Watsonulus cf. W. eugnathoides (Fig. 14A). The general shape of the dermosphenotic can be seen in the holotype but is incompletely preserved.

Upper jaw.- The premaxilla appears to be similar to that in the undetermined parasemionotid of Patterson (1975) but bears at least ten large pointed teeth (Fig. 15B). The maxilla is long and is deeper than in W. cf. W. eugnathoides, but is notched in a similar manner posteriorly. The length of the maxilla makes up 37 to 48 percent of the total length of the skull. The ratio of the depth of the maxilla to the length of its dentigerous portion is 0.22 to 0.29.

There are approximately 55 teeth on the maxilla; these are larger anteriorly than posteriorly. The shallow supramaxilla is slightly less than half the length of the toothed portion of the maxilla. These bones are lightly ornamented.

Lower jaw.- The lower jaw is short and stout, rising steeply to a high coronoid process. The dentary bears at least 25 large sharp teeth. Externally an angular and a surangular are visible (Fig. 16A). Internally a

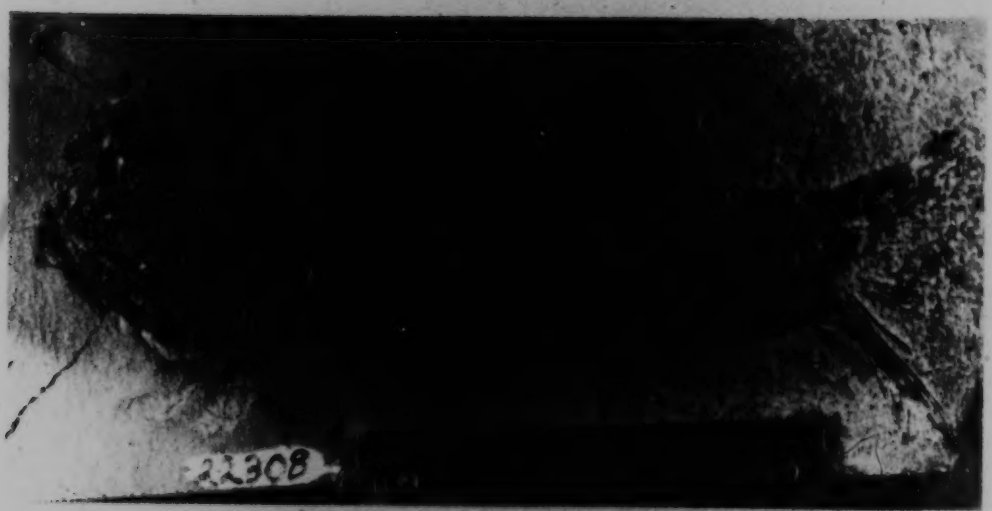


Fig. 15: Laudonia brevicephala gen. et sp. nov.
A. Complete specimen UAVP 22308 (holotype).
B. Smooth-On peel of the skull of UAVP 22301.
(Abbreviations are listed on p. xiv).

prearticular and at least one coronoid can be seen that bear many very small teeth (Fig. 16B). The angular is highly sculptured but the dentary only moderately so.

Opercular series.- The preopercle of Laudonia is most similar to that of Ospia but is longer along its ventral border (Fig. 11). It is much shorter than the preopercle in Watsonulus. The angle between the vertical and horizontal pit lines is acute as in Watsonulus. The posterior border is thickened for the sensory canal and the anteroventral border is notched. The ratio of the length of the maxilla to the depth of the preopercle is 0.76 to 0.85, less than this ratio in Watsonulus cf. W. eugnathoides.

The opercle is slightly concave on its anterior border and convex posteriorly. It is deeper than long. The ratio of the length of the opercle to the length of the skull is 0.43 to 0.45. The subopercle is approximately the same size as the opercle and has an upturned projection at its anteroventral corner that fits between the opercle and preopercle (Fig. 14). The border between the opercle and subopercle is strongly convex downward, then straightens out and angles sharply posterodorsally. The interopercle is triangular and small. These bones are all covered by a moderate sculpture of tubercles and ridges.

There are 11 or 12 branchiostegals. The most anterior of these is thickened and may be identified as a lateral gular. The median gular is oval but is slightly wider

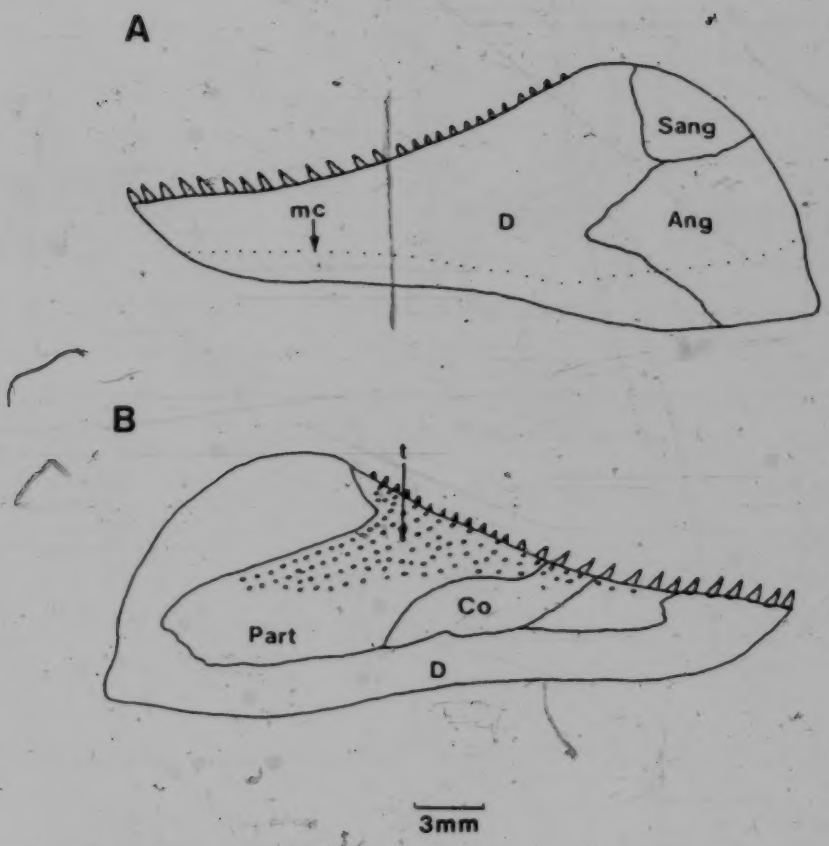


Fig. 16: Left lower jaw of Laudonia brevicephala gen. et sp. nov.
A. Lateral view (UAVP 22301).
B. Medial view (UAVP 22301).
(Abbreviations are listed on p. xiv).

posteriorly than anteriorly (Fig. 15B). It is ornamented with radiating ridges and does not resemble the gular described by Olsen (1984) and Lehman (1952) for Watsonulus, where the median gular is hourglass- or diamond-shaped.

Palate.- Except for a vomer (Fig. 15B), the bones of the palate are not preserved. This bone is displaced as Olsen (1984) mentioned for his specimens of Watsonulus. It is small and bears about ten teeth.

Pectoral girdle.- The cleithrum and supracleithrum are typical of the family; the clavicle has not been recognized. There are two extrascapulars, the dorsal is long and oval and the ventral, almost square. These bones bear typical ornament.

Paired fins.- The pectoral fins bear 14 or 15 lepidotrichia and are relatively short, extending to the origin of the pelvic fins (Fig. 15A). The ratio of the length of the pectoral fin to standard length is 0.195 to 0.203. The pelvic fins are small and are located about midway between the pectoral fins and the anal fin (Fig. 15A). There are at least seven lepidotrichia.

Median fins.- The dorsal fin originates slightly posterior to the midpoint along the length of the body, in front of the level of the origin of the anal fin. There are five fringing fulcra on the anterior border of the fin and approximately 16 lepidotrichia. The anal fin bears 12 or 13 lepidotrichia. The caudal fin has 16 lepidotrichia

above the midline. Several large basal fulcra occur in front of each of these fins.

Squamation.- The bodies of these fishes are covered with typical parasemionotid scales that are deeper than long on the anterior part of the body and longer than deep on the posterior part. They are serrated along the posterior edge over most of the body. There is a total of approximately 40 rows of scales. The dorsal fin has its origin at about row 25 and the anal fin originates at about row 19 or 20. Additional meristic and morphometric data are provided in Table 2 and Appendix 2.

Discussion.- Laudonia shows a suite of characters that is not found in any of the described genera of parasemionotids. Its narrow preopercle, long, deep maxilla and characteristic opercle and subopercle distinguish it from all other members of the family.

Table 2

Summary statistics of morphometric and meristic data for *Laudonia*, *Albertonia cupidinia* and *A. lambei*

All proportional measurements presented as means with number of observations and ranges in parentheses. All measurements in mm. Abbreviations are listed on p. 10-12.

	Laudonia	*A. cupidinia*	*A. lambei*
SL	126(2;123-128)	227(3;198-242)	229(5;211-260)
HL	36(4;27-40)	72(5 60-91)	67(5;60-76)
HL/SL	.32(2;.31-.32)	.30(2;.29-.30)	.29(5;.26-.32)
HD	30(4;21-34)	54(4;45-64)	42(5;38-52)
HD/HL	.82(4;.79-.85)	.74(4;.69-.82)	.63(5;.55-.70)
BD	41(2;40-41)	83(2;63-102)	67(5;60-75)
BD/SL	.32(2;.32-.33)	.36(3;.32-.43)	.29(5;.27-.32)
MD/ML	.25(4;.22-.29)	.25(5;.20-.27)	.20(5;.15-.28)
ML/POPD	.82(4;.77-.85)	.81(5;.72-.88)	.96(5;.90-1.02)
OPL/OPD	<1(4)	<1(5)	>1(5)
OPL/HL	.45(3;.43-.45)	.43(4;.40-.47)	.51(5;.47-.57)
ML/HL	.44(4;.38-.48)	.42(4;.40-.44)	.42(5;.35-.46)
TS	40	40-42	40-41
SDF	24-25	25-29	25-27
SAF	19-20	22	22-23
P_1F	14-15	19-21	15-20
P_2F	7	13	7-8
DR	13-16	17	14-16
AR	13	15	13
CR	16	16	16
PL/SL	.20(2)	.49(2;.37-.61)	.41(5;.36-.46)

Genus Albertonia Gardiner, 1966

1916 Elonichthys (in part) Lambe, p. 39

1936 Dollopterus (in part) Berg, p. 166

1966 Albertonia Gardiner, p. 65

Type species.- Albertonia cupidinia (Lambe, 1916) from the Lower Triassic of Massive, Alberta, Canada.

Age range.- Early Triassic.

Distribution.- Lower Triassic of Alberta and British Columbia, Canada.

Revised diagnosis.- Large, deep-bodied parasemionotid. Pectoral fins greatly elongated, comprising at least 35 percent of standard length. Pectoral fins broad, bearing at least 18 lepidotrichia. Suspensorium nearly vertical or inclined slightly forward. Preopercle large and unreduced with convex anterior margin. Suborbitals lacking. Premaxilla with 12 or 13 large, pointed teeth. Maxilla relatively long, reaching to anterior border of preopercle. Supramaxilla deep; anterior half much deeper than posterior half.

Discussion.- The large unfragmented preopercle distinguishes Albertonia from all other parasemionotids except Watsonulus. Albertonia differs from other Canadian parasemionotids by its larger size and long, broad pectoral fins. The supramaxilla in Albertonia also differs from that in Watsonulus and Laudonia. In the two latter genera, the supramaxilla is approximately the

same depth for its complete length. In Albertonia, however, the anterior half of the supramaxilla is about twice as deep as the posterior half.

Albertonia cupidinia (Lambe, 1916)

Figs. 17, 18.

1916 Elonichthys cupidineus Lambe, p. 39, pl. 2

1917 Elonichthys cupidineus Lambe, p. 293.

1925 Elonichthys cupidineus Raymond, p. 553 (name only).

1929 Elonichthys cupidineus Hay, p. 690.

1936 Dollopterus cupidineus Berg, p. 166.

1937 Dollopterus cupidineus Aldinger, p. 206.

1966 Albertonia cupidinia Gardiner, p. 65.

1976 Albertonia cupidinia Schaeffer and Mangus, p. 548, fig. 18.

Holotype.- NMC 757, 757a, fragment of trunk with nearly complete pectoral fin, part and counterpart, from the Lower Triassic of Massive, Alberta.

Type locality.- Railway cut on the line of the Canadian Pacific Railway near Massive, Alberta, approximately 21 km west of Banff, Alberta (51°13.5'N, 115°47.8'W).

Distribution.- Lower Triassic of Alberta and British Columbia, Canada.

Referred specimens.- NMC 9964, 12330 (12332, counterpart of 12330) and 12331, all from the railway cut at Massive.

Specimens from the Wapiti Lake area that resemble Albertonia cupidinia in the shape of the skull bones and in the shape of the body are also referred to this species (UAVP 19027, 22555, UC 1160 and NMC 12328). Other specimens from Wapiti Lake are tentatively referred to this species based mainly on head and body shape (UAVP 18964, 22292, TMP 84.42.3, 84.42.50, 84.42.51, 84.42.52 and 84.42.54).

Revised diagnosis.- Deep-bodied Albertonia. Pectoral fins long, reaching up to 60 percent of standard length. Body depth 32 to 45 percent of standard length. Head relatively short and deep; depth reaching 75 to 80 percent of length. Premaxilla with 13 large, pointed teeth. Maxilla deep (depth approximately 25 percent of length of dentigerous portion), with many small, pointed teeth. Ratio of length of maxilla to depth of preopercle 0.70 to 0.85. Length of opercle approximately 40 to 47 percent of length of head. Subopercle slightly smaller than opercle; opercle deeper than long. Border between opercle and subopercle angled sharply posterodorsally. Anal fin with about 15 lepidotrichia.

Description.- The following description is based almost entirely on the specimens from the type locality.

Albertonia cupidinia is a large, deeply fusiform parasemionotid with greatly elongated pectoral fins (Fig. 18A). The standard length is approximately 200 to 250 mm. The skull is short and deep. The ratio of the depth of the

skull to its length is 0.74 to 0.82. The ratio of the depth of the body to the standard length is 0.32 to 0.42 and the maximum body depth is approximately 100 mm.

Skull roof.- The bones of the skull roof are covered with a sculpture of tubercles and ridges, but the specimens from the type locality are badly weathered so it is difficult to make out the details of the sculpture. The skull bones of specimens from Wapiti Lake are covered by a very coarse sculpture of tubercles (Fig. 18B). The exact shapes of the roofing bones are difficult to ascertain but they appear to be of the typical shapes and relationships described for the other members of the family.

At least four canal-bearing infraorbitals form the posterior and ventral borders of the orbit. The posterior ones overlap the anterior border of the preopercle. Two supraorbitals are present. The anterior one is rectangular and the posterior one is squarish. The other bones surrounding the orbit are the antorbital anteroventrally and the dermosphenotic posterodorsally. The dermosphenotic is narrow and bears the infraorbital canal (Fig. 17A).

Upper jaw.- The premaxilla is partially covered by the antorbital so its exact shape cannot be determined. It bears at least 13 fairly large, pointed teeth, many of which are not visible in lateral view. The maxilla is about 40 percent of the length of the skull. Its ratio of depth to length is 0.25 to 0.27. There are many small, pointed teeth along the ventral edge of the maxilla. The supramaxilla is approximately half the length of the

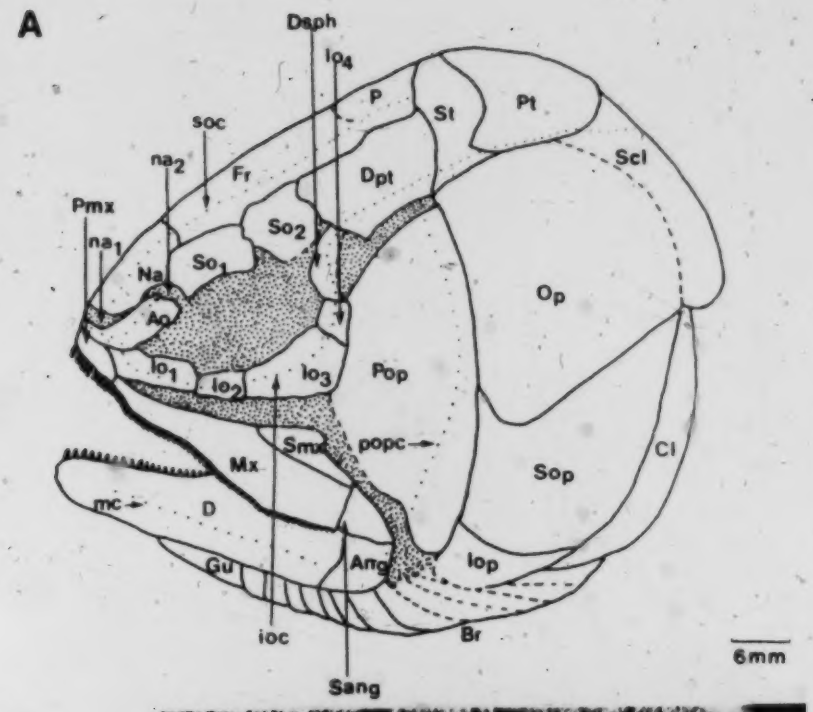
toothed portion of the maxilla and is deepest just anterior to its midpoint. The anterior half of this bone is deeper than the posterior half.

Lower jaw.- The lower jaw is deep and robust and of the typical holostean type. It bears many small teeth, approximately the same size as those seen on the maxilla. Nothing is known of the medial bones of the lower jaw.

Opercular series.- The exact shape of the preopercle in the specimens from the type locality cannot be determined but it appears to be broad. In the specimens from Wapiti Lake, the preopercle is as broad as in any parasemionotid (Fig. 18B). The posterior border is thickened for the preopercular canal in the usual way. The ratio of depth of preopercle to length of maxilla is 0.72 to 0.83. The length of the opercle makes up approximately 40 to 47 percent of the length of the skull. The subopercle is smaller than the opercle and has a projection anterodorsally that fits between the preopercle and the opercle. The border between these two bones is convex downward anteriorly, then straightens out and angles strongly dorsoposteriorly. The interopercle appears to be relatively large but its shape is uncertain.

Pectoral girdle.- The cleithrum is "C-shaped" as in other members of the family, but the shape of the clavicle and extrascapulars is uncertain.

Paired fins.- The pectoral fins are very large (length up to 60 percent of the standard length) and reach



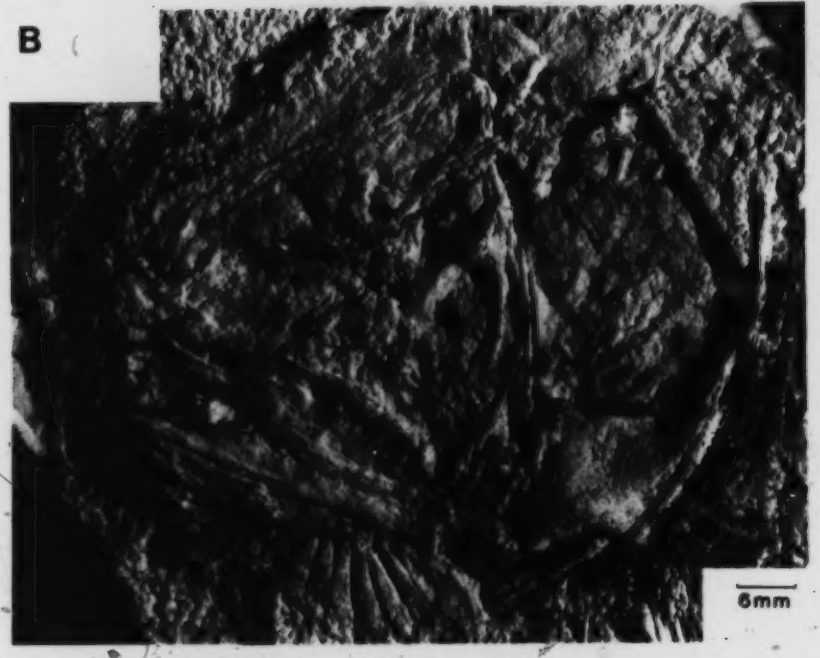


Fig. 17. Albertonia cupidinia (Lambe, 1916).
A. Composite drawing of the skull based mainly on NMC 9964.
B. Smooth-On peel of the skull of NMC 9964.
(Abbreviations are listed on p. xiv).

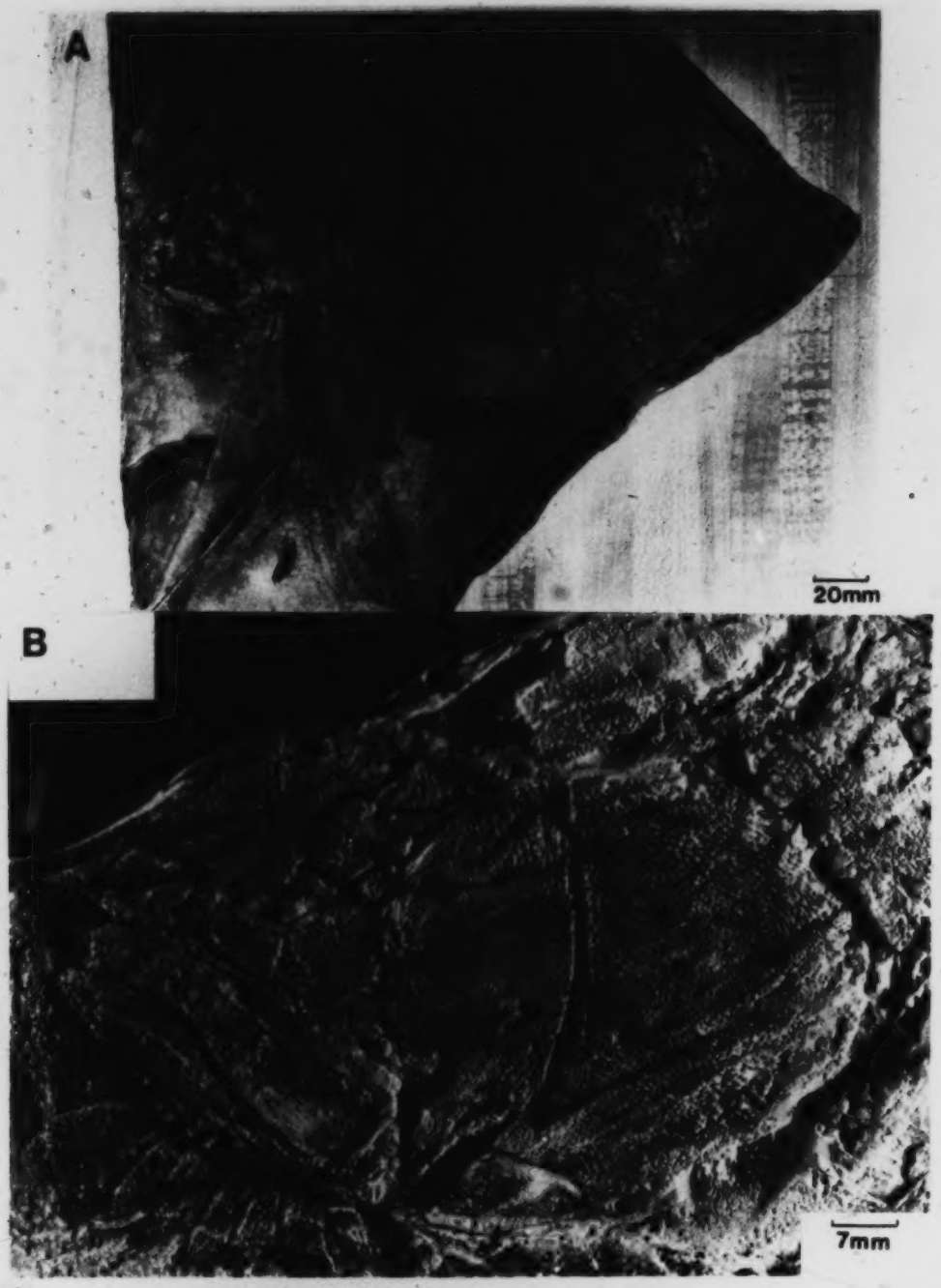


Fig. 18: Albertonia cupidinia (Lambe, 1916).
A. Complete specimen NMC 12330.
B. Smooth-On peel of the skull of UC 1160 from Wapiti Lake, B.C., referred to this species.
(Abbreviations are listed on p. xiv).

at least to the origin of the anal fin (Fig. 18A). They bear approximately 21 lepidotrichia. The pelvic fins are small and originate closer to the anal fin than to the pectoral fins. They bear 12 or 13 rays.

Median fins.- The dorsal fin is on the posterior half of the body and originates anterior to the level of the insertion of the anal fin (Fig. 18A). It bears 16 or 17 lepidotrichia. The anal fin bears about 15 lepidotrichia and the caudal fin bears 15 or 16 above the midline.

Squamation.- The scales are shaped like those in other parasemionotids. They are serrated posteriorly but ornament is not evident on the specimens studied. There are 40 to 42 rows of scales in total. The dorsal fin originates at row 25 to 27 and the anal fin originates at row 22 to 24.

Additional data on meristic and morphometric characters for this species are given in Table 2 and Appendix 2.

Discussion.- Albertonia cupidinia was first described as Elonichthys cupidineus by Lambe (1916) on the basis of a partial specimen consisting of only an incomplete body and a greatly elongated pectoral fin. His original classification of the species in the genus Elonichthys was tentative and based only on general body form and fin position.

Berg (1936) referred this species to the genus Dollopterus, which was believed to be a kind of flying

fish, because of its greatly enlarged pectoral fin. Based on additional material from western Canada, Gardiner (1966) recognized that this species was actually very different from Dollopterus. He erected the new genus Albertonia to contain it and suggested that Albertonia cupidinia was a perleidid.

Schaeffer and Mangus (1976) restudied the material of Albertonia cupidinia from the National Museums of Canada and recognized the presence of an interopercle and a supramaxilla. They referred the species to the family Parasemionotidae based on this information. I agree with their assignment of this species to the family Parasemionotidae based on the mixture of advanced and primitive characters. Although the material from Wapiti Lake referred to the species Albertonia cupidinia may show features that are not available in the original material, a more complete description of this species must await the collection of better preserved material from the type locality.

Albertonia lambei sp. nov.

Figs. 19, 20.

Holotype.- TMP 84.42.56A, a complete skull and skeleton from the Lower Triassic Sulphur Mountain Formation of British Columbia, Canada. Purchased from René Vandervelde by the Tyrrell Museum of Palaeontology in 1984.

Etymology.- After L.M. Lambe, who originally described the genus Albertonia.

Type locality.- C cirque on the Ganoid Range in the Wapiti Lake area of eastern British Columbia, Canada (54°32.2'N, 120°44.1'W).

Distribution.- Lower Triassic of British Columbia, Canada.

Referred specimens.- UAVP 22291, 22293, 22294 and TMP 85.42.16A. Additional specimens referred mainly on the basis of size and general shape of the body and head are UAVP 22290, TMP 83.206.28 and 84.42.55.

Diagnosis.- Large, moderately deep-bodied Albertonia. Pectoral fins long, reaching 35 to 45 percent of standard length and reaching to origin of anal fin. Body shallow, body depth 25 to 32 percent of standard length. Head relatively long and shallow, head depth 55 to 70 percent of skull length. Ratio of length of maxilla to depth of preopercle approximately one. Premaxilla with 12 large, pointed teeth. Ratio of depth of maxilla to length of maxilla 0.15 to 0.25; maxilla with 55 to 60 teeth.

Subopercle approximately same size as opercle; opercle longer than deep. Length of opercle approximately 47 to 56 percent of length of skull. Anal fin with 13 lepidotrichia.

Description.- Standard length of these fishes is approximately 250 mm but it reaches as much as 370 mm. The ratio of depth of skull to length of skull is 0.55 to 0.70. The maximum body depth is 60 to 80 mm and the ratio of body depth to standard length is approximately 0.30.

Neurocranium.- The neurocranium is not preserved but part of the parasphenoid can be seen in some specimens and appears to be like that in other members of the family.

Skull roof.- Bones of the skull roof are covered with a heavy sculpture of tubercles and ridges. The posttemporal, supratemporal, parietal, dermopterotic, frontal and nasal are similar to those seen in other members of the family. The frontal is long and meets the diamond-shaped nasal just medial to the anterior supraorbital (Fig. 19A). The dermopterotic is short and deep.

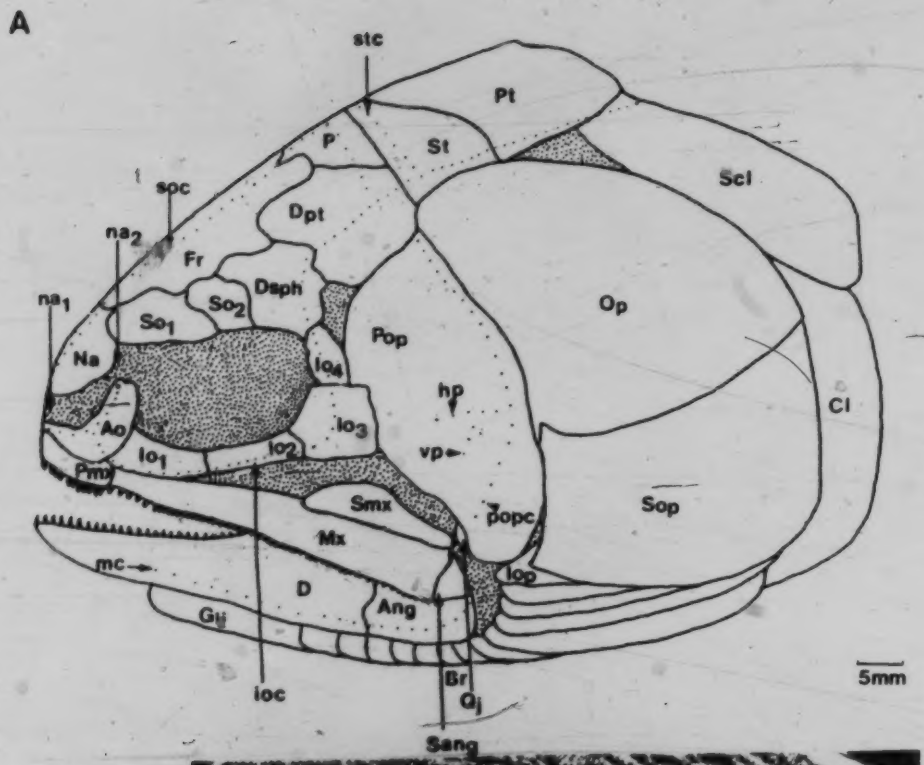
There are four infraorbitals along the ventral and posterior borders of the orbit (Fig. 19). The anterior one is fairly long and shallow, the second is a tube surrounding the sensory canal and the third is the largest and is square. The fourth infraorbital is small and square. The anterior supraorbital is shallow and long and the posterior one is rectangular to diamond-shaped. The antorbital is very similar to the one found in

Watsonulus but its expanded posterior portion is somewhat longer (Fig. 20B). The infraorbital canal travels through all of these bones.

Upper jaw.- The premaxilla is very similar in shape to that described by Patterson (1975) for the undetermined parasemionotid (Fig. 20B). It bears 12 large teeth. The length of the maxilla is 35 to 45 percent of the length of the skull and has a depth to length ratio of 0.14 to 0.24. There are 55 to 60 pointed teeth along its ventral edge that decrease in size toward the posterior end of the bone. The supramaxilla is similar to the one in A. cupidinia.

Lower jaw.- The lower jaw is shallower than that seen in Albertonia cupidinia and is of the typical shape described for the other species in the family. The prearticular can be seen in one specimen and is very similar to that described for Watsonulus (Olsen, 1984).

Opercular series.- The preopercle is large and unreduced. Its anterior margin is convex for most of its length but becomes concave ventrally and is notched slightly on its anteroventral edge. The highest point is at the posterodorsal edge where the preopercular canal begins (Fig. 19A, 20B). The posterior edge of the preopercle is convex for its entire length and the ventral border is also convex. The preopercular canal and vertical and horizontal pit lines are like those described for Watsonulus. The ratio of the depth of the preopercle to



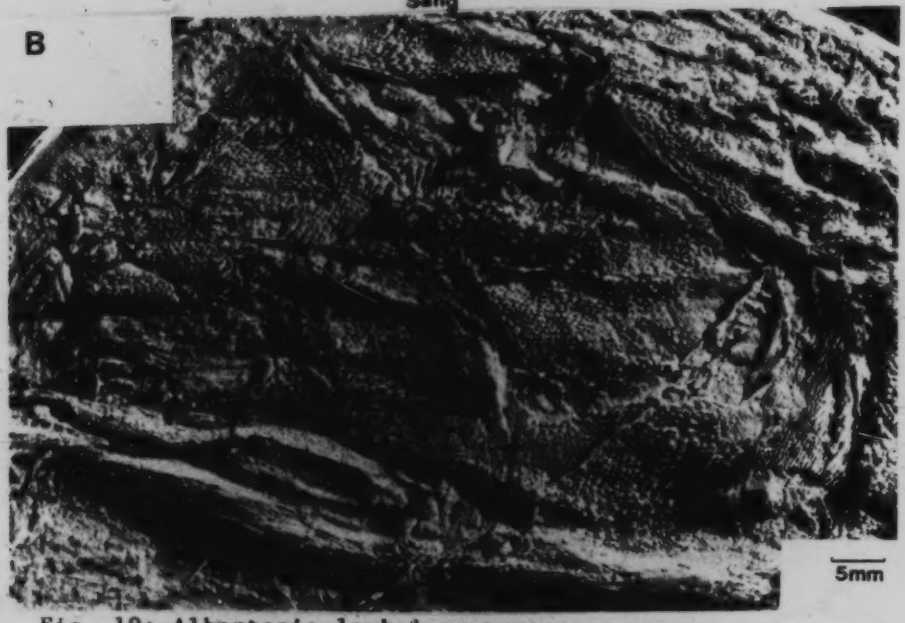


Fig. 19: Albertonia lambei sp. nov.
A. Composite drawing of the skull based on TMP 84.42.56A (holotype) and UAVP 22293.
B. Smooth-On peel of the skull of TMP 84.42.56A.
(Abbreviations are listed on p. xiv).

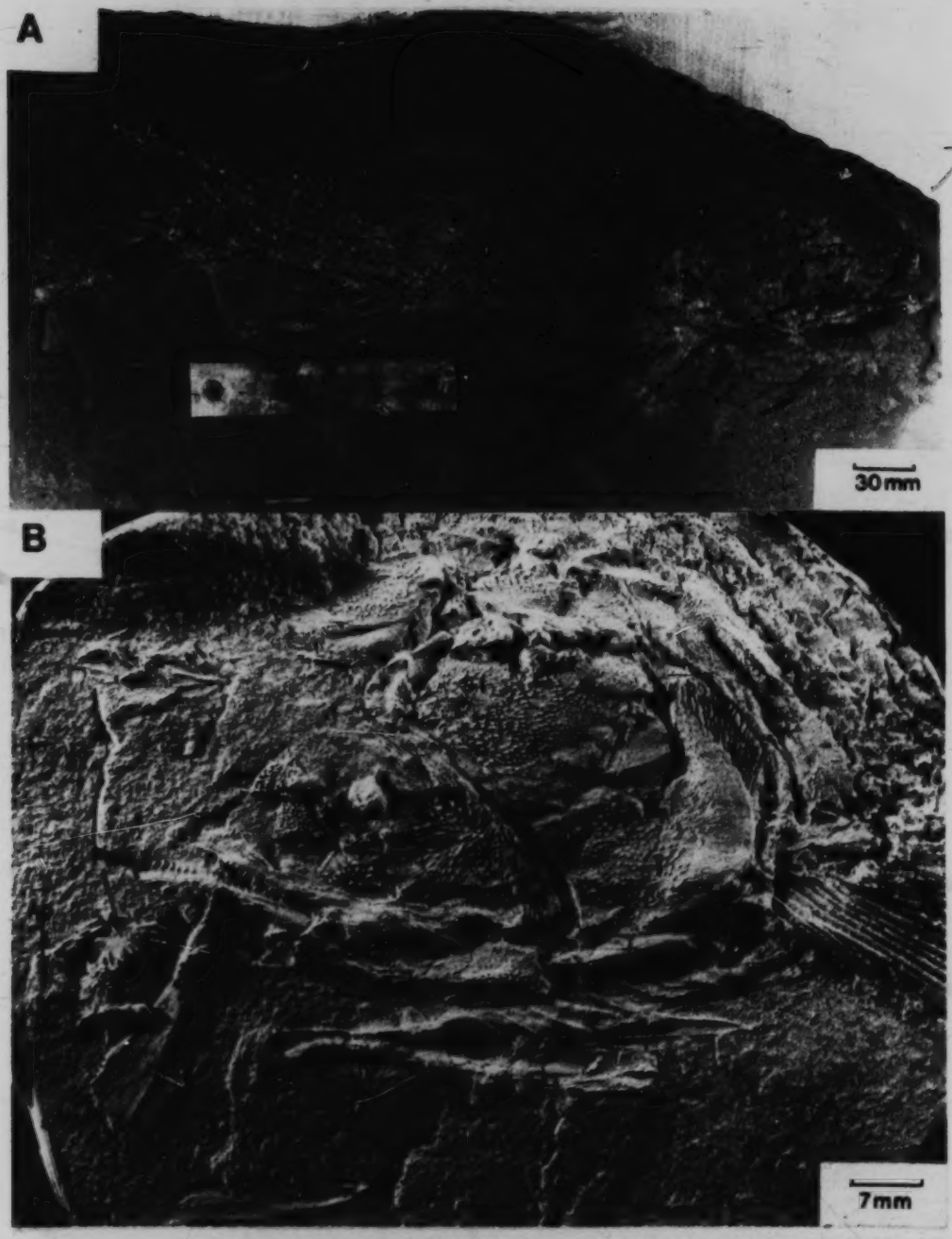


Fig. 20: Albertonia lambei sp. nov.
A. Complete specimen TMP 84.42.56A (holotype).
B. Smooth-On peel of the skull of UAVP 22293.
(Abbreviations are listed on p. xiv).

the length of the maxilla is approximately one.

The opercle and subopercle are very large and subequal in size. The opercle is longer than deep. The dorsal and ventral borders of this bone are convex and the anterior border is concave. The border between the opercle and subopercle is slightly convex downward. The subopercle has a small projection that inserts between the opercle and preopercle and another small projection that overlaps the interopercle (Fig. 19A). The ratio of length of opercle to length of skull is 0.47 to 0.56. The interopercle is triangular and small.

The gular plate is oval and bears a cross-shaped ornament near its anterior border (Fig. 20B). There are about ten branchiostegal rays.

Paired fins.- The pectoral girdle is as described for the other species in the genus.

The pectoral fins are long, reaching to the origin of the anal fin (Fig. 20A). The ratio of length of pectoral fins to standard length is 0.35 to 0.45. There are approximately 20 lepidotrichia on each pectoral fin. The pelvic fins are small and originate slightly closer to the anal fin than to the pectoral fins. The pelvic fins bear approximately eight lepidotrichia.

Median fins.- The dorsal fin originates on the posterior half of the body just behind the level of the origin of the pelvic fins and in front of the level of the origin of the anal fin (Fig. 20A). It bears approximately

16 lepidotrichia. The anal fin is far back on the body and bears 12 or 13 lepidotrichia. The caudal fin bears 15 or 16 lepidotrichia above the midline.

Squamation.- The scales are of the typical parasemionotid type. There are 40 to 41 rows of scales. The dorsal fin originates at row 25 or 26 and the anal fin originates at row 22 or 23.

Additional meristic and morphometric data are listed in Table 2 and Appendix 2.

Discussion.- Albertonia lambei is similar to A. cupidinia in its large size, deep body and greatly elongated pectoral fins. The shape of the preopercle is similar but the exact shape of this bone in Albertonia cupidinia is unknown.

A number of differences occur between these two species, especially in the shape and proportions of some of the skull bones and in the overall depth of the body and head. The skull and body are longer and shallower in A. lambei than in A. cupidinia. The relative length of the pectoral fins is less in A. lambei (Fig. 4) although there is overlap between the two species in this character. The ratio of the length of the maxilla to the depth of the preopercle is approximately one in A. lambei and 0.70 to 0.85 in A. cupidinia. The ratio of the depth of the maxilla to the length of the maxilla is 0.15 to 0.25 in A. lambei, and the maxilla bears approximately 55 to 60 teeth. In A. lambei, the ratio of the depth of the maxilla to its length is higher,

averaging at least 0.25, and the maxilla bears approximately 75 teeth. The opercle is longer than deep in A. lambei and deeper than long in A. cupidinia. The anal fin bears 13 lepidotrichia in A. lambei, 15 in A. cupidinia.

5. Discussion of Phylogeny

A) Relationships of the Perleididae and Parasemionotidae

1) Family Perleididae

The family Perleididae has been suggested to be a possible sister group of all holostean and teleostean fishes, including the family Parasemionotidae (Schaeffer, 1973; Gardiner, 1960, 1984). Gardiner (1984) lists five shared derived characters of perleidids and non-chondrostean actinopterygians:

1. Elongate upper caudal fin-rays.
2. Dorsal and anal fin-rays equal in number to their supports.
3. Antorbitals and premaxillae present.
4. Premaxillae with an internal (nasal) process which lines the nasal pit.
5. A dilator fossa.

If the family Perleididae is, in fact, a close primitive relative of holostean and teleostean fishes, then the features that are shared among perleidids and all higher actinopterygians can be considered primitive for higher fishes. Features that holostean and teleostean fishes do not share with the perleidids may be derived in either group. This makes the perleidids a potentially useful outgroup for studying neopterygian relationships.

2) Family Parasemionotidae

Although the importance of the intermediate position of the family Parasemionotidae is fairly well understood, the exact phylogenetic relationships of this family are not certain. The family has variously been considered of chondrostean, subholostean or holostean grade. It has been placed as the sister group of all other higher actinopterygians (Olsen, 1984), of the amiid and teleost line (Gardiner, 1967) or of the amiid line directly (Patterson, 1973). In order to understand its phylogenetic position the exact nature of its primitive and advanced features must be better understood. The family Perleididae may be used to help establish the polarities of some of the character states in the parasemionotids.

Patterson (1973) suggested grouping all of the more advanced actinopterygian fishes into one large taxon based on their possession of the following characters:

1. Body lobe of the tail reduced so that the outer principal rays of the upper lobe of the caudal fin are approximately equal in length to those of the lower lobe.
2. Fin rays equal in number to their endoskeletal supports in the dorsal and anal fins.
3. Premaxilla with an internal process lining the anterior part of the nasal pit.
4. Vomer differentiated and moulded to the underside of

the ethmoid region.

5. Articular with a coronoid process.
6. Suspensorium vertical or nearly so.
7. Preopercular with a narrow dorsal limb.
8. Symplectic developed as an outgrowth of the hyomandibular cartilage.
9. Upper pharyngeal dentition consolidated.
10. Clavicles lost or reduced to one or more plates overlying the postbranchial lamina of the cleithrum.

Patterson (1973) used the name Neopterygii, following Nelson (1969) and Regan (1923), for this group, which included the teleosts, gars, amiids, caturids, parasemionotids, oligopleurids, semionotids, pycnodonts, gyrodonts, coccodonts and luganoiidids. All more primitive fishes not possessing the characters in the above list were placed in the infraclass Chondrostei.

The perleidids also possess several of the characters in the above list so these features are probably not synapomorphies for the Neopterygii, but for a larger group including the perleidids. The characters that perleidids share with neopterygians are: elongate upper caudal fin rays, unpaired fins with rays that equal their supports and premaxillae with internal processes that line the nasal pit. The other characters in the list are not present in the perleidids so they may be useful synapomorphies for the Neopterygii.

The parasemionotids possess most of the characters in the above list although the clavicles are still fairly

large and some members of the family retain broad preopercles. The vomers are present but they are only weakly attached to the ethmoid region of the skull and are easily displaced (Fig. 15B; Olsen, 1984). The presence of upper pharyngeal dentition has not yet been detected.

The preopercle shows a trend toward reduction and fragmentation within the family Parasemionotidae (Lehman, 1952; Lehman, et al., 1959) and in some the neopterygian condition of the preopercle has been reached. I therefore agree with Patterson (1973) with respect to his placement of the parasemionotids in the infraclass Neopterygii, but certainly near its base.

At the same time, Patterson placed parasemionotids along with teleosts, amiids, caturids, oligopleurids and semionotids into the division Halecostomi based on the following characters:

1. Median neural spines present, at least in the caudal region.
2. Maxilla mobile, free from cheek, with a peg-like internal head.
3. Supramaxilla present.
4. Interopercle present.
5. Myodome large.
6. Large post-temporal fossa without an endoskeletal roof.
7. Intercalar with membranous outgrowths over the surface of the otic region.

8. Quadratojugal lost as an independent element.
9. Epibranchials with uncinate processes at their upper ends.

These features separate this group from the division Ginglymodi, which includes the gars. The perleidids show none of the features in the above list. The parasemionotids actually only show features 2-4 of the above list. They retain an independent quadratojugal (Fig. 12; Lehman, 1952; Olsen, 1984) and have a smaller myodome and post-temporal fossa than in other halecostomes (Patterson, 1973). The intercalar has only the most rudimentary membranous outgrowths (Patterson, 1973; 1975) or lacks them altogether (Olsen, 1984). The states of characters 1 and 9 are presently not known for the parasemionotids. Despite this Patterson concluded that there are good reasons for including the parasemionotids in the Halecostomi.

Patterson goes on to suggest that the parasemionotids should be placed in the subdivision Halecomorphi along with the amiids and caturids. Of his list of eight characters that unites the halecomorphs and separates them from the teleosts, only one is present in parasemionotids. This is the form of the jaw joint in which the symplectic and quadrate each fit into an articular facet on the articular bone. This double jaw joint is a characteristic of Amia and its relatives and on this evidence the parasemionotids are related to Amia according to Patterson (1973) and Bartram (1977). Patterson does admit,

however, that "An articulation between the symplectic and articular is interpreted as a specialization only as a working hypothesis. If this should prove to be a wrong assumption, the parasemionotids cannot yet be assigned to either of the major groups of Halecostomi and the halecomorphs must be characterized at the caturid level by the form of the intercalar." (Patterson, 1973).

Olsen (1984) disagreed with Patterson's classification of the parasemionotids and suggested a very different set of relationships. In his view the possession of two primitive features, the retention of the clavicles and the broad dorsal limb on the preopercle in Watsonulus, place this genus and its relatives in a critical position for establishing polarities of characters in other groups of neopterygians. He stated that because of the retention of these features, characters shared by Watsonulus and other neopterygians must be primitive for neopterygians (Olsen, 1984). The most critical of these characters is the nature of the jaw joint. If the type of jaw joint expressed by Watsonulus (and therefore Amia) is primitive, then a whole different system of relationships arises.

Olsen (1984) cites some support for the suggestion that this double jaw joint is primitive. He looked at the jaw joint in Birgeria and refers to the descriptions of Pteronisculus (Nielsen, 1942) and Boreosomus and Birgeria (Nielsen, 1949). In these genera, the

symplectic articulates with the lower jaw (Nielsen, 1942), which may suggest that this system is primitive.

"We can conclude from this discussion that if the broad dorsal limb of the preopercular and the unreduced clavicles of Watsonulus are primitive characters shared with chondrosteans, and reduction of these characters to the condition seen in Amia happened only once within Neopterygii, the nature of the jaw joint of Watsonulus and Amia must be a shared primitive character for neopterygians and possibly for actinopterygians as a whole. The nature of the jaw joint in gars and teleosts must be derived. Amia must, therefore, represent the sister-group of the clade containing both gars and teleosts, and Watsonulus must be the sister-group of the clade containing Amia, gars and teleosts" (Olsen, 1984).

One of the important questions then is whether the jaw joint seen in Watsonulus and Amia is a character state primitive for the Neopterygii (and possibly for actinopterygians as a whole) or whether it is an advanced character seen only in one group. Gardiner (1984, p. 346) points out that the symplectic referred to by Nielsen for Pteronisculus is actually an interhyal. This interhyal is also present in Recent chondrosteans as a hypertrophied cartilage and is often incorrectly referred to as a symplectic (Gardiner, 1984, p. 357). He says that the symplectic (interhyal) of Pteronisculus and the symplectic seen in neopterygians are not homologous and the symplectic of neopterygians is synapomorphous for this

group (Gardiner, 1984, p. 359). If this is true then the double jaw joint probably does suggest a relationship between the parasemionotids and the halecomorphs, and the jaw joint seen in gars and teleosts may be the primitive condition. If the double jaw joint is primitive as Olsen suggests, then there is no special relationship between the parasemionotids and the halecomorphs. This would place the parasemionotids in the division Halecostomi, *incertae sedis* as to subdivision. Unfortunately, nothing is known of the nature of the jaw joint in perleidids, so they are not helpful in resolving this problem.

Olsen (1984) also questions the validity of the division Halecostomi. This group is based on a number of characters that unite the amiid-caturid line with teleosts, and separate them from the gars. If the *Amia-Watsonulus* jaw joint is primitive and the one seen in gars and teleosts is advanced, then gars and teleosts would be more closely related, not halecomorphs and teleosts, and the division Halecostomi would not be valid. Besides the structure of the jaw joint, however, Olsen has no other characters to unite gars and teleosts as sister-groups. As pointed out earlier, the validity of this synapomorphy is in doubt, so the relationship between gars and teleosts is tenuous.

Since there is disagreement about the relationships among the parasemionotids, halecomorphs, gars and teleosts, it is difficult at the present time to place the

parasemionotids into any taxon at the divisional or subdivisional level of Patterson (1973). I suggest that this family be left as Neopterygii *incertae sedis* until these questions have been resolved.

B) Present Status of the Family Parasemionotidae

1) *Historical*

The family Parasemionotidae was first erected by Stensio (1932) for the genus *Parasemionotus* Piveteau, 1929 from Madagascar. He did not give a diagnosis for this family, but at the same time he erected the family Ospifdae to include the genera *Ospia* and *Broughia* from East Greenland. He gave a fairly detailed description of the family Ospiidae, which was suggested to be closely allied to parasemionotids, but distinct, mainly because of the lack of an interopercle in the ospiids. These families both were characterized by a combination of primitive and advanced characters and were assigned a position near the base of the higher actinopterygians.

Piveteau (1934) described the genus *Watsonulus* from Madagascar and assigned it to the family Parasemionotidae. He included a more formal diagnosis for this family and noted the close similarity between parasemionotids and ospiids. Nielsen (1936) pointed out that Stensio had noted the presence of an interopercle in his Greenland genera following the publication of their descriptions, so

Nielsen suggested that the two Greenland forms be lumped with the two Madagascar genera in the family Parasemionotidae.

Lehman (1952) described three more genera from Madagascar, Stensionotus, Jacobulus and Thomasinotus, which he assigned to the family Parasemionotidae. This was followed by the inclusion of Lehmanotus, Devillersia and Piveteaunotus (Beltan, 1968). These last three genera from Madagascar are all based mainly on structures of the neurocranium and little is known of the other features of their skeletons.

Patterson (1973) suggested that a group of genera that is usually placed in other families be placed in the family Parasemionotidae. He did not feel that there was any special relationship between these genera and the parasemionotids but said that because the family Parasemionotidae had come to be considered a grade group, with no synapomorphies to unite it, there was no advantage in limiting the grade too closely. He included Promecosomina Wade, 1935, Tungusichthys Berg, 1941 and Paracentrophorus Piveteau, 1939-40, three genera that are often placed in their own families. He also included Eoeugnathus Brough, 1939, Sinoeugnathus Su, 1959 and Allolepidotus Deecke, 1889, three genera that are generally placed in the family Caturidae. He stated that these three genera did not show the synapomorphies that unite the caturids with the amiids so they should be

relegated to the more primitive family.

Schaeffer and Mangus (1976) included the genus Albertonia from western Canada in the family Parasemionotidae and Griffith (1977) placed Phaidrosoma, a new genus that he described, in the family based on its general evolutionary grade. He also recommended that the genera Woodthorpea Swinnerton, 1925 and Archaeolepidotus Accordi, 1956, two genera usually placed in the family Semionotidae, be transferred to the family Parasemionotidae as Lehman (1966) and Patterson (1973) had suggested.

The family Parasemionotidae, as described above, includes all genera of halecostome grade that do not show specializations that would place them into one of the other described families. These genera do not have anything special in common except that they are at the same general grade of organization. Some genera are placed here simply because they are poorly known. I prefer the more restricted use of the family Parasemionotidae of Piveteau (1934) and Lehman (1952; 1966) and give a revised diagnosis for the family in an attempt to better clarify the criteria for membership in this family.

2) Revised diagnosis for the family Parasemionotidae

Body small to large, fusiform. Neurocranium ossified as single element. Posterior myodome and posttemporal fossa moderately developed. Parasphenoid relatively short, extending two-thirds of way along basioccipital. Hyomandibular facet nearly horizontal.

Posttemporal and supratemporal single paired elements, meeting at midline. Supratemporal with supratemporal canal. Frontal and dermopterotic large. Parietal small and squarish. Postrostral lost. Nasal very large, situated on dorsal side of ethmoid region and meeting counterpart at midline.

Orbit surrounded by series of bones. Posterior border composed of dermosphenotic and last few infraorbitals. Ventral border composed of first few infraorbitals; anterior border formed by first infraorbital, antorbital and first supraorbital. Supraorbitals and dermosphenotic making up dorsal border.

Interopercle present. Dorsal limb of preopercle fairly broad in some genera, fragmented in others. Ventral limb of preopercle vertically beneath dorsal limb.

Separate premaxilla present on each side of skull. Maxilla reduced in size, free from preopercle and infraorbitals, with anteromedial process that articulates with ethmoid region of skull. Supramaxilla present. Vomers only weakly attached to parasphenoid and easily displaced.

Lower jaw long and robust, coronoid process high.

Angular and surangular present. Branchiostegals fairly numberous; median and possibly lateral gulars present.

Clavicle retained, at least in some genera.

Lepidotrichia of fins equal in number to endoskeletal supports and unbranched for long proximal portion of length. Fulcral scales present. Abbreviated heterocercal tail; body lobe reduced, outer principle rays of upper lobe equal to those on lower lobe. Scales of reduced lepisosteid type, higher than long on anterior portion of body, becoming longer and lower posteriorly and ventrally.

3) Discussion

In the above diagnosis, the parasemionotids are defined by a combination of primitive and advanced characters. Characters that are primitive, separating the parasemionotids from other neopterygians, include:

1) Neurocranium ossified as a single element.
2) Relatively small posterior myodome and posttemporal fossa.
3) Comparatively short parasphenoid.
4) Dorsal limb of preopercle fairly broad in some genera. In those genera in which fragmentation of the dorsal limb occurs, the fragmented elements do not overlap the anterior portion of the remaining thickened part of the preopercle but abut against it. The combined shape of these bones retains the general outline of an unfragmented propercle.
5) Ventral limb of preopercle placed vertically beneath

dorsal limb. Ventral limb does not curve forward and extend further anteriorly than the dorsal limb and is not expanded.

6) Maxilla remains relatively long and deep.

7) Vomers only weakly attached to parasphenoid and easily displaced.

8) Clavicle retained, at least in some genera.

Advanced features of the family Parasemionotidae that unite it with derived neopterygians, and separate it from more primitive families, include:

1) Posterior myodome and posttemporal fossa present.

2) Hyomandibular facet nearly horizontal.

3) Postrostral lost.

4) Nasals very large, situated on dorsal side of ethmoid region and meeting at midline.

5) Antorbital present as separate element.

6) Interopercle present.

7) Fragmentation of dorsal limb of preopercle in some genera forming "suborbitals".

8) Premaxilla separate from rostral.

9) Maxilla reduced in size and free from preopercle and infraorbitals.

10) Supramaxilla present.

11) Vomers present and attached to parasphenoid.

12) Lower jaw with high coronoid process.

13) Lepidotrichia equal in number to their endoskeletal supports and unbranched for a rather long proximal

portion of their length.

14) Abbreviated heterocercal tail.

15) Scales of the reduced lepisosteid type.

Trends occur within the family Parasemionotidae, especially in the reduction and fragmentation of the preopercle (Fig. 21). In more primitive actinopterygians, the dorsal limb of the preopercle is broad, and is attached to the maxilla and infraorbitals. Within the family Parasemionotidae, fragmentation of the dorsal limb of the preopercle occurs (Gardiner, 1967) so that in some genera the preopercle more closely resembles that seen in more advanced fishes (Fig. 21). The bones produced by this fragmentation are variously called spiraculars, postorbitals, suborbitals or anamestic preopercular bones (Piveteau, 1934; Stensio, 1947; Lehman, 1952). These bones are not like the true suborbitals of higher fishes, however, and do not overlap the anterior portion of the remaining thickened part of the preopercle; instead they only abut against it (Gardiner, 1960). The combined shape of these bones retains the general outline of an unfragmented preopercle (Lehman, 1952).

If there is a problem about how to classify the parasemionotids, it is where to draw the limits of the family along the line of development of these trends. According to Ernst Mayr, "A family is a taxonomic category containing a single genus or a monophyletic group of genera, which is separated from other families by a decided gap" (Mayr, 1969, p. 94). I believe that those

genera that show extreme development or loss of a character resulting in the development of a pronounced gap between this subgroup and the main stem of the family should be placed in separate families.

Although, as Patterson (1973) suggested, there are no synapomorphies to unite the family Parasemionotidae, there is a unique combination of characters that establishes that the group is monophyletic in the sense of Mayr (1969). The members of the family have character combinations, including primitive and derived characters, that one would expect to find in the descendants of a common ancestor.

The definition of the family Parasemionotidae as a monophyletic group is based on systematic philosophy. In the true sense of cladistic monophyly, the family is a paraphyletic group and can therefore only be viewed as a grade. In the synthetic view however, not all descendants of the common ancestor must be included in a taxon beforeit is considered monophyletic. I believe it is most useful in the case of the family Parasemionotidae to place those genera that display extreme development of character trends in a separate family or separate families, and retain the family Parasemionotidae for those genera that are more conservative in their development of these features.

Fig. 21: Reduction, fragmentation and shape modification of the preopercle in the parasemionotiforms.

A. Perleidus canadensis.

B. Watsonulus cf. W. eugnathoides.

C. Laudonia brevicephala.

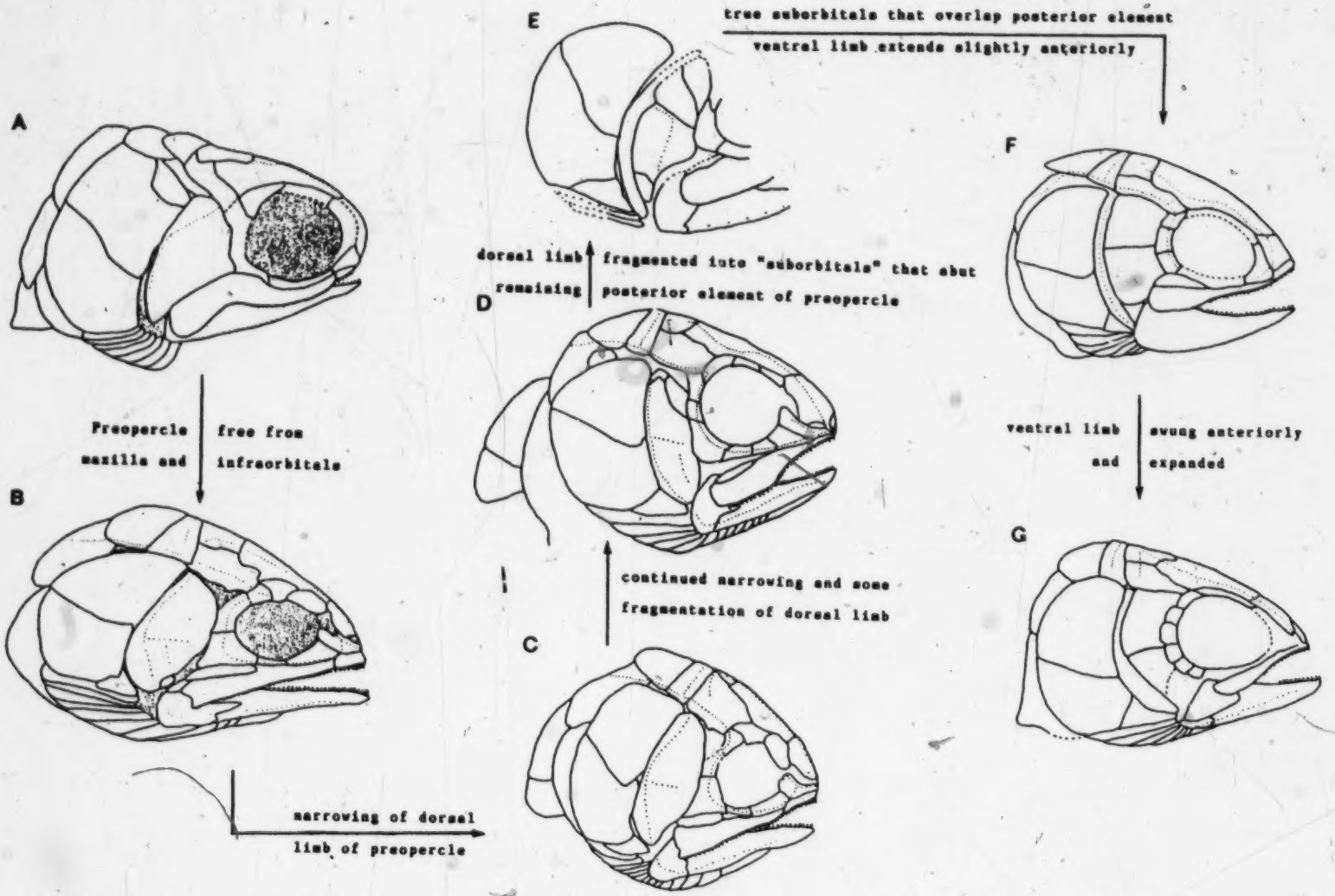
D. Parasemionotus labordei (after Lehman, 1952).

E. Thomasinotus divisus (after Lehman, 1952).

F. Promecosomina formosa (after Gardiner, 1960).

G. Phaidrosoma lunzensis (after Griffith, 1977).

(A= primitive condition for the higher actinopterygians; dorsal limb of preopercle expanded and attached to maxilla and infraorbitals; ventral limb vertically placed beneath dorsal limb. B-E= family Parasemionotidae).


A
Preopercle maxilla and
free from infraorbitals
B
narrowing of dorsal limb of preopercle
C
continued narrowing and some fragmentation of dorsal limb
D
dorsal limb remaining
fragmented into "suborbitals" that abut posterior element of preopercle
E
true suborbitals that overlap posterior element
ventral limb extends slightly anteriorly
F
ventral limb and
swung anteriorly expanded
G

4) Genera assigned to the family Parasemionotidae

If all of the genera that have been assigned to the family Parasemionotidae are compared to the revised diagnosis for the family given in the previous section, only the following genera can be retained: Parasemionotus, Watsonulus, Ospia, Broughia, Stensionotus, Jacobulus, Thomasinotus, Albertonia, Laudonia, and possibly Devillersia, Lehmanotus and Piveteaunotus.

Gardiner (1960, p. 342) showed that Promecosomina has large, well-developed, quadrangular suborbitals that overlap the anterior border of the preopercle (Fig. 21). The preopercle in this genus is narrow and reduced to only a thickened posterior border for the preopercular canal. Gardiner suggested that this is ample reason for separating this genus from the Parasemionotidae because in those parasemionotids in which suborbitals are developed, Jacobulus (Lehman, 1952, fig. 126) and Thomasinotus (Lehman, 1952, fig. 129; Lehman, et al., 1959, fig. 17), they retain the shape of the anterior part of the preopercle and only abut the anterior edge of the thickened part of the preopercle. They do not overlap the preopercle.

Patterson (1973) questioned Gardiner's interpretation of the fossils but said, "In my opinion this is a nice distinction to draw, given the state of preservation of the material of Promecosomina. If true, it would place

Promecosomina with Eoeugnathus, in which the preopercular is similarly overlapped" (Patterson, 1973).

The overlap of a narrow, thickened preopercle by suborbitals is also seen in Eoeugnathus (Brough, 1939), Phaidrosoma (Griffith, 1977) and Woodthorpea (Swinnerton, 1925). This is probably also true of Paracentrophorus (Gardiner, 1960) and Sinoeugnathus (Su, 1959), although it is not as well established in these two genera.

In typical members of the family Parasemionotidae, the ventral limb of the preopercle is vertically aligned with the dorsal and middle parts of the bone. In some of the genera that have been assigned to the family in recent years, however, the ventral limb of the reduced preopercle is swung anteriorly, often abutting against the posterior edge of the lower jaw and extending further anteriorly than the anterior margin of more dorsal parts of the preopercle. It may be expanded as in more derived actinopterygians. This condition is seen in Phaidrosoma, Woodthorpea and Sinoeugnathus, and is probably also true of Tungusichthys.

Other characters seen in some of the genera assigned to the family by Patterson and Griffith that are not consistent with the diagnosis of the family Parasemionotidae given above are the lack of a clavicle in Eoeugnathus (Brough, 1939), the lack of an articular process on the anterior portion of the maxilla in Phaidrosoma (Griffith, 1977) and large dorsal scales

that extend into stout sharp spines in Woodthorpea (Swinnerton, 1925).

I believe that because of the presence of the characters discussed above in the genera Promecosomina, Eoeugnathus, Phaidrosoma, Woodthorpea, Sinoeugnathus and possibly Paracentrophorus and Tungusichthys, these genera should be removed from the Family Parasemionotidae and placed in other taxa, possibly closely related to this family. Unfortunately, not enough is known of the genera Allolepidotus and Archaeolepidotus to make useful comments about them except that they may or may not belong in the family Parasemionotidae.

Some question exists as to whether genera such as Jacobulus and Thomasinotus should be included in the family Parasemionotidae because the state of development of the preopercle and suborbitals is approaching the condition seen in higher fishes (Fig. 21). Based on what is known of these genera, however, I believe that they are most similar to the parasemionotids and should remain, at least for now, in this family.

6. Conclusions

The first purpose of this study has been to supply detailed descriptions of Lower Triassic fishes from western Canada that have not previously been described. To this end, I have described five taxa in this project. The first of these, Perleidus canadensis, is a subholostean of the family Perleididae. The other four species belong to the family Parasemionotidae. One of these parasemionotids, Albertonia cupidinia, has previously been described, but only in a cursory manner. A second species, A. lambei has been added to the genus Albertonia. A third parasemionotid, Laudonia brevicephala, represents a new genus and species, and the fourth parasemionotid from western Canada has been tentatively assigned to Watsonulus cf. W. eugnathoides.

The second purpose of this project has been to comment on the phylogenetic relationships and generic composition of the family Parasemionotidae. The family Perleididae has been used to help establish the polarities of characters seen in the parasemionotids. Most important among these characters are the structures of the cheek region, the jaws and the ethmoid region of the skull. Through the study of the states of these characters in the perleidids and parasemionotids, the phylogenetic relationships of the family Parasemionotidae discussed by

Patterson (1973), Olsen (1984) and Gardiner (1984) have been tested. Unfortunately, controversy regarding the exact relationships of the parasemionotids has not been settled, but I believe that Patterson's ideas about their relationship to the caturid-amiid line are more likely to be correct than is Olsen's suggestion that parasemionotids occupy a more basal position in the evolution of higher actinopterygians.

The main support for Patterson's view is the structure of the double jaw joint of halecomorphs and parasemionotids. Gardiner (1984) showed that Olsen's (1984) suggestion that the double jaw joint is a primitive character, is invalid and the special relationship between gars and teleosts that Olsen suggests has little, if any, basis.

Finally, the generic composition and monophyletic nature of the family Parasemionotidae have been discussed. The trend in the reduction and fragmentation of the preopercle that has been identified by many authors, including Gardiner (1967) and Lehman (1952), is central to the discussion of where the limits of the family Parasemionotidae should be drawn. It has been shown that one criterion for inclusion in the family Parasemionotidae is the absence of true suborbitals that overlap the preopercle. If this is taken to be a valid point of separation between the family Parasemionotidae and closely related groups, then the family can be more easily

defined. The second character that is useful for defining the family Parasemionotidae is the nature of the ventral limb of the preopercle. In parasemionotids, the ventral limb of the preopercle is placed vertically beneath the dorsal limb, while in some of the genera that have been incorrectly assigned to this family the ventral limb curves forward toward the lower jaw, extending further anteriorly than the dorsal limb. With further study more differences between the parasemionotids and their close relatives should be identified.

The family Parasemionotidae has been shown to be monophyletic in the sense of Mayr (1969) in that it exhibits the combination of characters one would expect to find in the descendants of a common ancestor.

This project is the first of many that I hope to undertake on the Lower Triassic fishes from western Canada. At the Wapiti Lake sites alone there are as many as twenty different taxa of fishes that have not been dealt with in any detail. As collection at the sites continues, continued diversity is realised. I hope to undertake the study of more of these fishes as I feel they are an important contribution to the knowledge of Lower Triassic fish diversity. One of the major tasks that is necessary at this stage is the detailed quarrying of intact strata on the Ganoid Range. This will help to establish the age of the rocks that contain these fossils more accurately and will identify any differences in age of the taxa that occur within the Vega-Phroso Siltstone

Member of the Sulphur Mountain Formation.

Additional work is also needed in the study of the family Parasemionotidae from western Canada and from other parts of the world. A revision of the genus Watsonulus is necessary, and a review of type material of all genera is in order. I believe that this kind of a study is important because I feel that the family Parasemionotidae will continue to be a central point of interest for those workers searching for the ancestry of the higher actinopterygian fishes.

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Introduction to Appendix 1

Appendix 1 presents morphometric and meristic data for the genus Watsonulus obtained from the literature and from specimens. In many cases, measurements have been taken from published photographs. The following list cites the sources of the data listed in Appendix 1.

Specimen number or shorthand used	Source
TYPE A (pl.7)	Piveteau's Type A- description and pl. 7 of Piveteau (1932)
TYPE A (pl.9)	Piveteau's Type A- description and pl. 9 of Piveteau (1932)
TYPE B (pl.8)	Piveteau's Type B- description and pl. 8 of Piveteau (1932)
TYPE C (pl.7)	Piveteau's Type C- description and pl. 7 of Piveteau (1932)
TYPE A (pl.1)	Piveteau's Type A- description and pl. 1 of Piveteau (1939-40)
BM(NH) P16628	Lehman's Type 2- description and pl. 38 of Lehman (1952)
BM(NH) P16629	Lehman's Type 2- description and pl. 39 of Lehman (1952)
EM	Lehman's Type 3- description and pl. 42 of Lehman (1952)
Leh. (pl.7)	Specimen from southwestern Madagascar- description and pl. 7 of Lehman, et al. (1959)
Leh. (pl.8)	Specimen from southwestern Madagascar- description and pl. 8 of Lehman, et al. (1959)
Leh. (pl.9)	Specimen from southwestern Madagascar- description and pl. 9 of Lehman, et al. (1959)
YPM 8994	Description and fig. 4 of Olsen (1984)

Specimen number or shorthand used	Source
YPM 8996	Description and fig. 15 of Olsen (1984)
AMNH 11732	Original specimen
AMNH 11734	Original specimen
UAVP 19125	Original specimen
UAVP 19124	Original specimen
UAVP 19128	Original specimen
TMP 84.42.2	Original specimen
NMC 10113	Original specimen
UC 1156	Original specimen

Appendix 1

Morphometric and meristic data on *Watsonulus*

Part 1

Specimen #	SL	HL	HL/SL	HD	HD/HL	BD
TYPE A (pl.7)	-	51	-	32	.627	-
TYPE A (pl.9)	155	45	.29	34	.756	47
TYPE B (pl.8)	122	38	.31	23	.613	35
TYPE C (pl.7)	85	30	.35	19	.633	-
TYPE A (pl.1)	-	-	-	40	.702	-
BM(NH) P16628	-	37	-	27	.735	-
BM(NH) P16629	-	36	-	29	.824	-
EM	-	36	-	22	.609	-
Leh. (pl.7)	-	22	-	14	.663	-
Leh. (pl.8)	-	22	-	14	.669	-
Leh. (pl.9)	-	23	-	15	.660	-
YPM 8994	-	30	-	28	.715	-
YPM 8996	-	-	-	-	-	-
AMNH 11732	-	32	-	20	.619	-
AMNH 11734	-	30	-	24	.800	-
UAVP 19125	132	43	.33	24	.547	31
UAVP 19124	-	55	-	30	.536	-
UAVP 19128	-	46	-	24	.527	-
TMP 84.42.2	173	51	.30	30	.588	36
NMC 10113	138	42	.30	23	.548	24
UC 1156	80	28	.35	17	.660	18

(All measurements in mm; abbreviations are listed on p. 10-12)

Appendix 1

Morphometric and meristic data on Watsonulus

Part 2

Specimen #	BD/SL	MD/ML	ML/POPD	OPL/OPD	OPL/HL
TYPE A (pl.7)	-	.25	.936	<1	.451
TYPE A (pl.9)	.303	-	-	-	.467
TYPE B (pl.8)	.283	.16	1.152	>1	.453
TYPE C (pl.7)	-	-	-	=1	.367
TYPE A (pl.1)	-	-	-	=1	-
BM(NH) P16628	-	.22	1.213	<1	.366
BM(NH) P16629	-	.24	.993	<1	.444
EM	-	.22	1.128	>1	.368
Leh. (pl.7)	-	.27	.775	=1	.411
Leh. (pl.8)	-	-	-	=1	.383
Leh. (pl.9)	-	.28	.818	<1	.380
YPM 8994	-	.17	1.079	=1	.440
YPM 8996	-	-	.970	-	-
AMNH 11732	-	.27	.957	<1	.413
AMNH 11734	-	.27	.917	=1	.433
UAVP 19125	.231	[illegible]	1.093	>1	.395
UAVP 19124	-	.16	1.275	>1	.294
UAVP 19128	-	.21	1.258	>1	.286
TMP 84.42.2	.207	.18	1.140	>1	.314
NMC 10113	.174	.21	1.130	>1	.405
UC 1156	.220	.19	1.040	>1	.400

Appendix 1

Morphometric and meristic data on Watsonulus

Part 3

Specimen #	ML/HL	TS	SDF	SAF	P1R	P2R	DR	AR	CR	PL/SL
TYPE A (pl.7)	.431	-	-	-	-	-	-	-	-	-
TYPE A (pl.9)	-	40	24	18	15	-	16	12	-	-
TYPE B (pl.8)	.507	50	29	26	-	-	12	11	13	-
TYPE C (pl.7)	-	34	-	-	-	-	-	-	13	-
TYPE A (pl.1)	-	-	-	-	-	-	-	-	-	-
BM(NH) P16628	.502	-	-	-	-	-	-	-	-	-
BM(NH) P16629	.504	-	-	-	-	-	-	-	-	-
EM	.414	-	-	-	-	-	-	-	-	-
Leh. (pl.7)	.358	-	28	24	10	-	15	-	-	-
Leh. (pl.8)	-	-	28	24	-	-	-	-	-	-
Leh. (pl.9)	.360	-	28	24	-	-	-	-	-	-
YPM 8994	.451	-	-	-	-	-	-	-	-	-
YPM 8996	-	-	-	-	-	-	-	-	-	-
AMNH 11732	.350	-	-	-	-	-	-	-	-	-
AMNH 11734	.367	40	25	19	-	-	-	-	-	-
UAVP 19125	.407	40	23	18	-	-	17	12	15	.189
UAVP 19124	.464	-	-	-	-	-	-	-	-	-
UAVP 19128	.429	-	-	-	-	-	-	-	-	-
TMP 84.42.2	.480	40	25	20	15	-	-	-	-	.209
NMC 10113	.405	39	24	20	-	-	-	-	-	.163
UC 1156	.436	39	25	20	15	9	16	13	15	.138

Appendix 2

Morphometric and meristic data for *Laudonia* and *Albertonia*

Part 1

Specimen #	SL	HL	HL/SL	HD	HD/HL	BD	BD/SL
Laudonia							
UAVP 22301	-	38	-	31	.827	-	-
UAVP 22308	128	40	.31	34	.850	41	.320
UAVP 22310	123	39	.32	32	.808	40	.325
UC 1191	-	27	-	21	.794	-	-
A. cupidinia							
NMC 12330	240	70	.29	-	-	102	.425
NMC 12331	198	60	.30	45	.742	63	.318
NMC 9964	-	62	-	51	.815	-	-
UAVP 22555	-	91	-	64	.703	-	-
UAVP 19027	242	-	-	-	-	-	.343
UC 1160	-	78	-	54	.686	-	-
A. lambei							
TMP 84.42.56A	215	68	.32	38	.551	60	.280
UAVP 22291	232	66	.28	39	.591	62	.265
UAVP 22293	228	60	.26	42	.700	70	.307
UAVP 22294	211	64	.30	38	.598	67	.315
TMP 85.42.16A	260	76	.28	52	.684	75	.289

(All measurements in mm; abbreviations are listed on p. 10- 12.)

Appendix 2

Morphometric and meristic data for *Laudonia* and *Albertonia*

Part 2

Specimen #	MD/ML	ML/POPD	OPL/OPD	OPL/HL	ML/HL
Laudonia					
UAVP 22301	.22	.850	<1	.453	.453
UAVP 22308	.29	.792	<1	.450	.475
UAVP 22310	.22	.850	<1	-	.436
UC 1191	.25	.769	=1	.434	.377
A. cupidinia					
NMC 12330	-	-	-	-	-
NMC 12331	.25	.828	<1	.400	.442
NMC 9964	.27	.722	<1	.468	.419
UAVP 22555	.20	.841	<1	.472	.411
UAVP 19027	.27	.800	-	-	-
UC 1160	.25	.875	<1	.397	.404
A. lambei					
TMP 84.42.56A	.28	.923	>1	.471	.353
UAVP 22291	.15	.902	>1	.470	.417
UAVP 22293	.17	1.000	>1	.567	.450
UAVP 22294	.24	.931	=1	.520	.425
TMP 85.42.16A	.15	1.020	=1	.514	.458

Appendix 2

Morphometric and meristic data for *Laudonia* and *Albertonia*

Part 3

Specimen #	TS	SDF	SAF	P1R	P2R	DR	AR	CR	PL/SL
Laudonia									
UAVP 22301	-	25	20	-	-	15	-	-	-
UAVP 22308	40	25	20	15	7	16	13	16	.203
UAVP 22310	40	25	19	14	-	13	-	-	.195
UC 1191	-	24	-	14	7	-	-	-	-
A. cupidinia									
NMC 12330	42	29	22	21	13	17	15	-	.610
NMC 12331	40	25	-	-	-	-	-	16	.370
NMC 9964	-	25	22	-	-	-	-	-	-
UAVP 22555	-	26	-	19	-	-	-	-	-
UAVP 19027	-	-	-	19	-	-	-	-	-
UC 1160	-	-	-	-	-	-	-	-	-
A. lambei									
TMP 84.42.56A	41	26	23	19	-	15	13	-	.396
UAVP 22291	40	27	22	18	-	16	13	16	.358
UAVP 22293	40	25	22	15	8	-	13	-	.382
UAVP 22294	41	26	22	-	-	16	-	-	.436
TMP 85.42.16A	41	26	23	20	7	14	-	-	.459